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# A Comparative Study of the Throat Musculature in the Plethodontidae of Mexico and Central America

BY

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Abstract: The paper treats, in detail, of the throat musculature of a number of free-tongued species of Mexican plethodontid salamanders representing the genera, *Bolitoglossa, Magnadigita, Pseudoeurycea, Lineatriton, Chiropterotriton, Parvimolge, Oedipina,* and *Thorius.* The various species in each genus are placed in species-groups, on the basis of similarity of structure, and the generic groups are compared. Some consideration is given to the phylogeny of the genera of the entire family Plethodontidae, based on the characters of the musculature as well as other general characters.

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## INTRODUCTION

The Plethodontidae of Mexico and Central America are in general a large and divergent group of free-tongued salamanders. The distribution of this group extends from the Mexican plateau south to the northern Andes and the Amazon basin. Within this vast area there are at present approximately ninety known species, some of which are as yet undescribed. In dealing with these salamanders, the early workers placed them in at least five genera (*Oedipus, Bolitoglossa, Oedipina, Haptoglossa,* and *Thorius*). In the recent monograph of the family by Dunn (1926), all Mexican and Central American plethodontids of the above genera were placed in the genus *Oedipus.* More recently Taylor (1944) restudied these salamanders and not only recognized most of the earlier genera but also described four new genera (*Pseudoeurycea, Chiropterotriton, Parvimolge,* and *Magnadigita*).

I have not seen a representative of the genus *Haptoglossa.* The type of the single species *pressicauda* is lost, and other specimens have not yet been rediscovered. Since I am dealing herein only with the free-tongued species, the genera *Batrachoseps, Haptoglossa* and *Ensatina* are not considered in this study.

The primary purpose of this study is to determine whether or not there are sufficient differences in the throat musculature and the hyobranchial apparatus of the Mexican and Central American genera of the plethodontid salamanders to provide a taxonomic basis for the recognition of the genera, and to show the intrageneric and intraspecific relationships as they are reflected by modifications of the throat myology. My studies have revealed convergences and parallel developments, and I have attempted to correlate these as far as possible with responses to the environmental factors.

The hyobranchial apparatus and the throat musculature of the Mexican and Central American plethodontid salamanders have received relatively little attention from anatomists until recent time. This fact is particularly true with reference to the myology, since only five species have been previously studied, representing approximately six percent of the species known to inhabit this wide area. The earliest account of the throat musculature of a plethodontid was that given in 1875 by Wiedersheim for the single European representative of the family, *Hydromantes genei.* Most of the early myological studies of salamanders were made by European workers on the genus *Salamandra,* a close but primitive relative of the Plethodontidae. These early investigations, while not establishing reliable homologies between groups, did provide the terminology to be used and established a basis for comparison. More recently, "The Anatomy of the Salamanders," by Eric T. B. Francis (1934), has provided a complete anatomical study of the species *Salamandra salamandra.* This work has been of immeasurable value in my studies of plethodontid myology.

The first study dealing with the throat myology of an American plethodontid appears to be that of Emerson (1905) on *Typhlomolge rathbuni.* This species is, however, a perennibranchial salamander, and the study has therefore little application to the present investigation.

An extensive work by Edgeworth (1911) describes and compares the development of the throat muscles from the fishes to the mammals. Edgworth's work is not directly concerned with the plethodontids except as they are similar to *Triton,* but it does deal with various aspects of muscle origin, development and homology, some of which will be considered hereinafter.

In 1920 Miss Louise Smith gave for the first time a detailed account of the hyobranchial musculature of a reasonably specialized plethodontid, in her study entitled "The Hyobranchial Apparatus of *Spelerpes bislineatus.*" Equally important to the study of comparative myology was Smith's comparison of the conditions found by Wiedersheim in *Hydromantes* with those of Druner (1904) in *Salamandra maculosa,* and these in turn with the throat myology obtaining in *Eurycea bislineata.* These comparisons and the resulting choice of morphological names represent the first real attempt to arrive at the muscle homologies between the Plethodontidae and the more primitive Salamandridae. Smith also described for the first time the MM. gularis, geniohyoideus medialis and the geniohyoideus lateralis, all of which are peculiar to the family Plethodontidae. The M. subarcualis rectus I (Smith's ceratohyoideus internus) is described in detail, as are other throat muscles of both the larva and adult.

The work by I. W. Wilder (1925) is in reality a confirmation of the work done earlier by Miss Smith and does not add to the known myological facts. The monograph of the family Plethodontidae by Dunn (1926) is almost entirely taxonomic. The short discussion on the myology is very general and is of no particular value to the present study. However, certain distributional and habitat notes are valuable.

By far the most important paper dealing with the comparative myology of the plethodontids is the work, "A Comparative Study of the Hyobranchial Apparatus and Throat Musculature in the Plethodontidae," published in 1935 by Jean Piatt. The study includes an investigation of at least one species and often a comparison of two or more, of all the then accepted genera, save *Leurognathus.* Piatt's purpose was "to furnish an anatomical basis for a slightly different interpretation of the phylogeny within the family Plethodontidae."

According to Piatt the family is divisible into five major groups as follows:

A. *Desmognathus* group, including *Desmognathus* and *Leurognathus.*
B. *Stereochilus* group, including *Stereochilus*, *Typhlotriton* and *Typhlomolge.*
C. *Gyrinophilus* group, including *Gyrinophilus, Pseudotriton, Eurycea* and *Manculus.*
D. *Plethodon* group, consisting of *Plethodon, Hemidactylium, Ensatina* and *Aneides.*
E. *Oedipus* group, including *Hydromantes, Batrachoseps* and *Oedipus.*

The two genera in group A are very closely related to each other but are obviously not closely related to the genera in any of the other groups. In group E, the allying of *Batrachoseps* with "*Oedipus*" is not proved, and it is a very questionable relationship. As to the relationships of the genera in groups B, C, and D, I have no opinion, since these genera have not been included in this study.

Of the numerous species in the genus *Oedipus* Tschudi, since shown to be preoccupied by *Oedipus* Berthold, (Taylor, 1940:408, Roberts, 1941: 26) and also to be a composite of eight genera, (Taylor 1944:188-232), Piatt examined only five of the eighty known species, and these belong to only three of the eight genera recognized by Taylor (1944). Furthermore, the species of *Oedipus* studied by Piatt were myologically at, or at least near, the two extremes of specialization in that genus. *Pseudoeurycea bellii* and *Magnadigita subpalmata* are two generalized species having few specialized muscles as compared with other species in these two genera, and they are also two of the few species, except for the species of *Thorius,* which do not have a well-developed intermandibularis anterior in all specimens. This fact may have contributed to Piatt's misidentification of the anterior slip of the intermandibularis posterior, for the more anterior muscle. The other three species, all belonging to the genus *Oedipina* (*uniformis, complex*, and *parvipes*), were considered by Piatt (1935:34) to be, on the basis of myology, coenotelic and worthy of reclaiming the name *Oedipina*, synonomized with the genus "*Oedipus*" by Dunn (1926: 432).

Piatt (1939, 1940) published two papers dealing with the "Correct Terminology in Salamander Myology." The first (1939), subtitled "Intrinsic Gill Musculature," is concerned with larvae and perennibranchial urodeles and is not pertinent to this study. His second study (1940), entitled "Transverse Ventral Throat Musculature," is a summary of muscle homologies, which has contributed greatly to a knowledge of the homologies of the transverse muscles. Certain of his conclusions have not been confirmed by my investigations, but these will be considered with the muscles involved.

Eaton (1937) reasoned that the most posterior of the transverse throat muscles should be called the gularis in all urodeles, and that the additional integumentary muscle of the Plethodontidae does not merit a separate name. His evidence was not sufficient to justify his conclusions, and I am convinced, as was Piatt (1940), that there are adequate reasons for retaining the term gularis for a muscle peculiar to the myology of the Plethodontidae. There are certainly five distinct transverse muscles in the adult plethodontids of Mexico and Central America. The gularis, geniohyoideus medialis, geniohyoideus lateralis, and quadrato-pectoralis are peculiar to the lungless salamanders and should not be confused with the analogous muscles of the Ambystomidae and Salamandridae.

Adams (1942) described and compared the hyobranchial apparatus and the throat musculature of *Hydromantes platycephalus* with that of *Hydromantes genei*. The works of Cope (1889) and Hilton (1909, 1946, and 1947) contain several plates showing the hyobranchial skeletons of many genera of plethodontids. Since Hilton's material included six of the currently recognized Mexican genera, his work has been frequently referred to, although there are certain details, particularly in the shape of the ceratohyals, which do not correspond to my observations.

Previous anatomical studies, which have included Mexican and Central American plethodontid salamanders, have been very incomplete and sketchy mainly because of the inadequacy of available material. In spite of the collections made by Dunn, Schmidt, Smith, Stewart, Taylor, and many others, there still remain many species known only by a few specimens, and there are yet areas in which little collecting has been done. Furthermore, there are few collections containing a series of plethodontid species sufficiently large to provide for an adequate anatomical study. Fortunately, however, there has been accumulated, over a period of years, mainly by the efforts of Dr. E. H. Taylor and Dr. Hobart M. Smith, a large collection of these salamanders in Doctor Taylor's private collections. A few specimens have also been available at the University of Kansas Museum of Natural History. Thus the availability of material as well as the need for further myological studies of these salamanders has been the major impetus for the undertaking of this paper.

## MATERIAL AND METHOD

The investigation embodied in this paper is based primarily on the Mexican and Central American Plethodontidae listed herein, although a number of other salamanders have been studied and used as comparative material. Considering the difficulties involved in collecting this type of material, I feel most fortunate in having had such an extensive collection, including at least one specimen of each of the species listed. *Haptoglossa* is the only genus occurring south of the United States which was not available for examination. The throat myology and hyobranchial apparatus of the following eight genera and fifty species has been studied. (Five undescribed species were studied but are not listed):

*Pseudoeurycea* Taylor
- *P. gadovii* (Dunn)
- *P. unguidentis* (Taylor)
- *P. smithi* (Taylor)
- *P. cephalica cephalica* (Cope)
- *P. bellii* (Gray)
- *P. gigantea* (Taylor)
- *P. cochranae* (Taylor)
- *P. robertsi* (Taylor)
- *P. leprosa* (Cope)
- *P. nigromaculata* (Taylor)
- *P. goebeli* (Schmidt)
- *P. rex* (Dunn)

*Chiropterotriton* Taylor
- *C. chiroptera* (Cope)
- *C. dimidiata* (Taylor)
- *C. chondrostega* (Taylor)
- *C. arborea* (Taylor)
- *C. terrestris* (Taylor)
- *C. lavae* (Taylor)
- *C. xolocalcae* (Taylor)
- *C. nasalis* (Dunn)
- *C. abscondens* (Taylor)
- *C. multidentata*

*Parvimolge* Taylor
- *P. townsendi* (Dunn)
- *P. richardi* Taylor

*Oedipina* Keferstein
- *O. uniformis* Keferstein
- *O. complex* (Dunn)
- *O. serpens* Taylor
- *O. syndactyla* Taylor
- *O. parvipes* (Peters)

- *Lineatriton* Tanner
  - *L. lineola* (Cope)
- *Magnadigita* Taylor
  - *M. nigroflavescens* (Taylor)
  - *M. macrinii* (Lafrentz)
  - *M. engelhardti* (Schmidt)
  - *M. rostrata* (Schmidt)
  - *M. franklini* (Schmidt)
  - *M. subpalmata* (Boulenger)
  - *M. dunni* (Schmidt)
  - *M. robusta* (Cope)
- *Bolitoglossa* Duméril and Bibron
  - *B. mexicana* Duméril and Bibron
  - *B. occidentalis* Taylor
  - *B. rufescens* (Cope)
  - *B. flaviventris* (Schmidt)
  - *B. striatula* (Noble)
  - *B. platydactyla* (Cuvier)
- *Thorius* Cope
  - *T. pennatulus* Cope
  - *T. dubitus* Taylor
  - *T. troglodytes* Taylor
  - *T. pulmonaris* Taylor
  - *T. narisovalis* Taylor
  - *T. minutissimus* Taylor
  - *T. macdougalli* Taylor

In addition I have dissected *Ambystoma texanum* (Matthes), *Salamandra salamandra* (Linnaeus), *Plethodon g. glutinosus* (Green), *Batrachoseps a. attenuatus* (Eschscholtz), *Gyrinophilus p. porphyriticus* (Green), *Eurycea l. longicauda* (Green), *Eurycea lucifuga* (Rafinesque), *Desmognathus f. fuscus* (Rafinesque), *Leurognathus m. marmorata* Moore, and *Hydromantes platycephalus* (Camp).

Comparisons have been made with the plates and figures of *Spelerpes bislineatus* prepared by Louise Smith (1920) *Salamandra* by Eric T. B. Francis (1935), *Hydromantes* by Lowell Adams (1942), Cranial muscles of the vertebrates by F. H. Edgeworth (1936), and Plethodontidae by Jean Piatt (1935). Those of Piatt have been particularly useful since there are a large number of genera figured, and one, *Oedipina parvipes,* has direct bearing on this investigation.

I was able to dissect the muscles quite successfully under a binocular microscope without recourse to the use of stains, except for a few muscles. When extremely small muscles could not be delimited or precisely determined, the muscle and the surrounding fascia were removed, stained in a seventy per cent alcohol solution of eosin, and studied under a compound microscope. Such a procedure was invaluable in determining whether or not the fibers of the M. intermandibularis anterior were continuous across the mid-ventral line or whether there was a median raphe present. The presence and extent of the M. rectus cervicis lateralis were also determined by this method. The use of eosin proved very successful in bringing out distinctly the muscle striations. By this method the muscle fibers were more heavily stained than was the fascia, so that they were readily discerned and could be followed with ease from origin to insertion. Furthermore, since the specimens were preserved in a seventy per cent alcohol solution, the staining could be done in a few minutes. The stained tissues were stored in small vials of dilute eosin solution from which they could be removed and studied as desired.

For each specimen studied in detail, the characteristics of fifteen throat muscles and of the hyobranchial cartilages were recorded. Each muscle was investigated to determine as accurately as possible the origin, insertion, size, shape, and relationships to other muscles. The position and extent of the muscles are all stated in terms of their relation to a common structure; for example, the mental symphysis or the posterior tip of the mandible. In no instance was an attempt made to determine the relative lengths of muscles between species, unless the difference in relative length was apparent. Though a study of the relative lengths of muscles may be desirable, its full usefulness as a character is not attainable unless sufficient individuals of each species are measured to determine the individual variation within a species. In most species examined I have seen only one specimen, and it has, therefore, not been possible to determine accurately the degree of variation among the individuals of a given species. I have utilized as characters only those muscle relations which seemed least variable. The relative lengths of the posterior segment of the M. rectus cervicis to the two anterior segments of the same muscle proved significant and was used throughout the study.

## MUSCLE TERMINOLOGY

The muscles examined are, except for the gularis, quadratopectoralis, geniohyoideus lateralis, and the rectus cervicis lateralis, homologous to the muscles of the more primitive *Salamandra.* It is for this reason that the work of Francis (1934) has been so useful in this study. The names of the muscles studied and the authority for each has been determined by usage and by the appropriateness of the term. I have followed for the most part the published studies of Francis, Drüner, Edgeworth, Smith, and Piatt in arriving at the terms used.

In order to prevent unnecessary repetition of characters common to most of the genera and to review briefly muscle homologies and authorities, the following list of throat muscles is presented in advance of the general description given for each genus studied.

### THE TRANSVERSE THROAT MUSCLES

*M. intermandibularis anterior* (Drüner 1901).

According to Piatt (1940:10) the intermandibularis anterior disappears completely at metamorphosis in the families Hynobiidae, Ambystomidae, Salamandridae and Plethodontidae, leaving the intermandibularis posterior as the most anterior of the transverse throat muscles. Although this may be true of the first three families, it is certainly not the condition in all genera of the family Plethodontidae. I have observed the anterior muscle in adults of at least one species of the following genera: *Pseudoeurycea, Chiropterotriton, Parvimolge, Magnadigita, Bolitoglossa, Oedipina, Batrachoseps* and *Lineatriton.* It was not present in the species of *Plethodon, Gyrinophilus, Eurycea* and *Hydromantes* which I examined. When present, this muscle lies along the anterior edge of the anterior slip of the intermandibularis posterior and is usually widest at the mid-ventral line. The muscle always arises in fascia a short distance medial to the mandible and is usually without a median raphe.

The fact that this muscle is absent in nearly all adult plethodontids living in the United States and is often absent in the two species (*Magnadigita subpalmata* and *Pseudoeurycea bellii*) studied by Piatt (1935:216) may explain in part the misunderstanding concerning this muscle in the family Plethodontidae.

In the family Desmognathidae a small straplike muscle extends from the mid-ventral line, immediately caudal to the symphysis, anterolaterad across the ventral surface of the mandible, and attaches to the anterolateral surface of the mandible. The median raphe is distinct, and there is a short distance separating this muscle from the anterior slip of the intermandibularis posterior. Whether the muscle described represents the intermandibularis anterior or a modification of the anterior part of the anterior slip of the intermandibularis posterior is as yet uncertain. Its position is, however, very suggestive of the intermandibularis anterior. Equally important is the fact that this muscle arises from the anterolateral surface of the mandible and extends across the ventral surface of the mandible. Such a condition is unique among the lungless salamanders and should be added to the family characteristics of Desmognathidae. Soler (1949) figures the superficial transverse throat muscle of *Desmognathus o. ochrophaeus* and represents this anterior muscle as I have found it in *Desmognathus f. fuscus* and *Leurognathus m. marmorata.*

*M. intermandibularis posterior* (Drüner 1901).

This muscle is always divided into a small anterior and a much larger posterior slip, both of which are fan-shaped, and together they occupy most of the area between the mandibular rami. Both arise from the dorsomedial surface of the mandible and insert in the ventral aponeurosis.

*M. gularis* (Smith 1920).

The gularis is a muscle peculiar to the plethodontids and is, according to Piatt (1935:223, 1940:10), a derivitive of the larval interhyoideus posterior, arising at the time of metamorphosis. The muscle takes its origin in fascia, with approximately the anterior half of the muscle arising in a thin sheet of fascia covering the greater part of the M. depressor mandibulae anterior. The major part of this thin sheet of fascia is in turn attached to a heavier fascia lying between the edges of the MM. depressor mandibulae and capiti mandibularis. The anterior fibers are usually not far posterior or anterior to the posterior tip of the mandible and their insertion is commonly at or near the mid-ventral line.

*M. depressor mandibulae* (Humphrey 1872).

In all genera of Mexican and Central American plethodontids, the depressor mandibulae is divided into two distinct muscles. Previous workers have referred to these divisions as slips, but this situation, in view of the entirely separated condition of the muscle, plus the fact that both muscles have very different origins and are separable from the origin to the insertion, is not representative of the true condition. I am therefore designating them as distinct muscles according to their position as the anterior and posterior muscle.

*M. depressor mandibulae anterior* (new name).

The anterior muscle arises from the squamosal and the lateral edge of the otic capsule. The part of the muscle arising from the otic capsule is usually deep to the M. cucularis major. The insertion is on the dorsal surface of the posterior tip of the mandible.

*M. depressor mandibulae posterior* (new name).

The posterior muscle arises from the fascia cephalodorsalis between the anterior muscle and the gular fold. It is entirely superior to the M. cucularis major. The insertion is on the ventral surface of the posterior tip of the mandible.

*M. quadrato-pectoralis* (Drüner 1901).

This muscle is large and is readily distinguished from the interhyoideus in all Mexican and Central American plethodontids. According to Piatt (1935:223) the quadrato-pectoralis "has not quite disappeared from even the specialized end genera, such as *Oedipus* and *Manculus*, but it has been so reduced functionally that its identity as a distinct element is almost negligible." Such a condition is not found in the Mexican and Central American species. I have found this muscle to be well developed, and its size indicates that it is a functional muscle. The variation in the point of origin has undoubtedly led to a masking of this muscle in many species, and I suspect, as in the case of *Hydromantes* and in other more northern genera, that the origin has shifted entirely to the ceratohyal and is therefore confused with that of the interhyoideus. If we accept Piatt's (1935 and 1940) reasoning that the interhyoideus posterior at metamorphosis is divided into two muscles, the gularis and the quadrato-pectoralis, and that the interhyoideus is retained in all plethodontids, then we have the conditions obtaining in the eight genera of Mexican and Central American Plethodontidae herein considered. This is in contrast to the more northern genera in which this muscle is lost (according to Piatt) in some, fused and nearly inseparable in others (*Hydromantes*) and having an entirely different arrangement in still others (*Aneides*).

In the Mexican and Central American genera, at least part of the origin of this muscle is always on the quadrate or the squamosal, but more often it arises from both bones. There are usually a few fibers arising from the tendinous sheath surrounding the ceratohyal at the point of its attachment onto the skull, but these fibers are always distinctly separated from the anterior fibers of the more posterior interhyoideus. In the more generalized species the origin is primarily, if not completely, on the posterior edge of the quadrate; this may justify, at least, the "quadrato" part of the name. The major part of the insertion is always in the ventral aponeurosis between the intermandibularis and the gularis.

*M. interhyoideus* (Drüner 1901).

The interhyoideus arises on the ceratohyal between the lateral curvature of the ceratohyal posterior to the caudal tip of the mandible and the attachment of the ceratohyal to the skull. The insertion is usually deep to the posterior slip of the intermandibularis posterior and is often broad and fan-shaped. This muscle in plethodontids has been found to be smaller than the quadrato-pectoralis and is unique in having a peculiar decussation of the fibers at or near its belly. Those fibers arising on the anterior edge of the muscle extend in a nearly transverse direction, whereas those on the posterior border extend in a nearly longitudinal direction and cross dorsally over the anterior fibers to insert as the anterior part of the muscle, thus reversing completely the order of the muscle fibers at the insertion. This one hundred and eighty degree rotation is present also in *Hydromantes* and may be used to separate the interhyoideus from the closely associated anterior fibers representing what remains of the quadrato-pectoralis in that genus.

### THE LONGITUDINAL AND DEEP MUSCLES

*M. geniohyoideus medialis* (Smith 1920).

The medialis arises from the posterior or ventral surface of the mandible lateral to the symphysis. The width of the origin is extremely variable. The lateral part of the insertion is on the ventral surface of the subarcualis rectus I, whereas the medial part is inserted along the anterior edge of the inscriptio tendinis. The lateral part of the insertion is usually posterior to the caudal tip of the mandible and is commonly lateral to the mid-ventral line.

The inscriptio tendinis is a connective tissue mass which lies in a more or less transverse position approximately ventral to the second ceratobranchial. It represents the ligamentous vestiges of the second basibrancial, often called the os thyroideum, and is a bony structure in some plethodontids. The inscriptio tendinis is an important structure and appears to serve a double function. It is first of all an area for insertion of the geniohyoideus medialis, the medial part of the subarcualis rectus I, the medial part of the rectus cervicis, and the small ventral slip of the abdominohyoideus. Secondly, it appears to serve as a transverse support for the throat region, since it is securely attached to the medial side of each subarcualis rectus I and also at the mid-ventral line. The condition described for *Hydromantes* by Adams (1924:189) is similar to that found in the Mexican and Central American genera.

*M. geniohyoideus lateralis* (Smith 1920).

The lateralis arises from the posterior, ventral and medial surfaces of the mandible and it is usually laterad and dorsad to the medialis. The extent of the attachment on the mandible is extremely variable. The insertion is on the lateral edge and on the dorsal surface of the ceratohyal. A few of the medial fibers are commonly extended posteriorly to the ceratohyal and are inserted on the floor of the pharynx.

The names of the geniohyoideus muscles here employed are those used also by Piatt (1940). Piatt has described the ontogenetic development of the geniohyoideus muscles in Plethodontidae in some detail, and I see no reason for questioning his reasoning and conclusions.

*M. rectus cervicis superficialis* (Edgeworth 1928).

The superficialis is a very thin sheet of muscle fibers arising entirely from the anterolateral edge of the sternum and becoming fused with the deeper profundus muscle at the first myocomma anterior to the sternum. This muscle is present in all genera of Mexican and Central American plethodontids studied, but is, at times, not easily separated from the profundus.

*M. rectus cervicis profundus* (Edgeworth 1928).

The major portion of this muscle is a direct anterior continuation of the rectus abdominis. It is inserted on the ventral surface of the subarcualis rectus I and along the posterior edge of the inscriptio tendinis.

*M. rectus cervicis lateralis* (new name).

In the course of this investigation it was noted that the M. omohyoideus is not present in the species of Plethodontidae of Mexico and Central America which I have examined. In *Salamandra salamandra* and *Ambystoma texanum* the omohyoideus arises from the medial surface of the ventral end of the scapula and is inserted along the lateral edge of the superficial portion of the M. rectus cervicis (fig. I). The anterior end of the insertion is at the level of the os thyroideum, whereas the posterior end is at the first myocomma of the rectus cervicis, anterior to the sternal cartilage. In these species the insertion is approximately twice the width of the origin.

A small slip of muscle arising on the edge of the sternum immediately laterad to the M. rectus cervicis superficialis, and extending anterolaterad to the lateral surface of the M. abdominohyoideus where it is inserted in fascia approximately at the level of the thyroid gland, was noted in most genera of Plethodontidae and in the family Desmognathidae. This muscle is not recognizable either in *Salamandra* or *Ambystoma,* but in *Desmognathus f. fuscus* it appears as a well-defined muscle extending from its origin on the sternum along the lateral edge of the rectus cervicis to the ventral surface of the medial end of the first ceratobranchial, where it is inserted (fig. 2). Particularly noteworthy is the presence of a myocomma anterior to the sternum, which corresponds to the first myocomma of the rectus cervicis. Equally significant is the insertion of the now reduced omohyoideus at the first myocomma of the lateral muscle. The muscles just described for *Desmognathus fuscus* are also present in *Plethodon g. glutinosus, Gyrinophilus p. porphyriticus,* and *Batrachoseps a. attenuatus* but are reduced in size, especially in *Batrachoseps.* In *Eurycea l. longicauda* the omohyoideus is further reduced, but its relationships remain unchanged. The lateral slip has also become reduced in size and is now inserted in the fascia on the lateral surface of the M. abdominohyoideus (fig. 3). In the case of the insertion the lateral slip has now reached a developmental stage comparable to the condition obtaining in the plethodontid genera of Mexico and Central America, and it is only a case of losing the small omohyoideus before reaching the condition existing in the genus *Pseudoeurycea* (fig. 4).

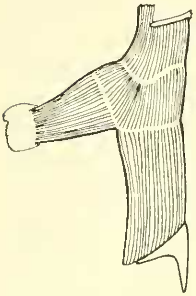

Fig. 1

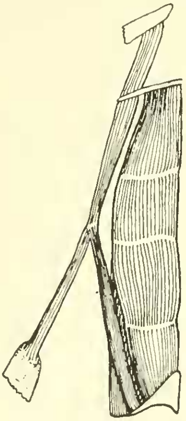

Fig. 2

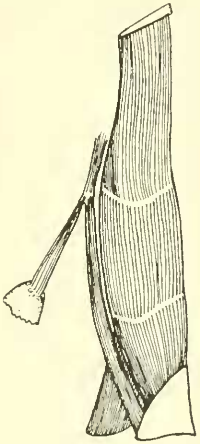

Fig. 3

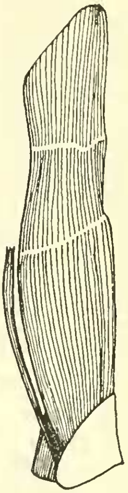

Fig. 4

FIG. 1. The muscle omohyoideus (left), and m. rectus cervicis in *Ambystoma texanum*. The m. rectus cervicis lateralis is absent.

FIG. 2. Characteristics of the m. rectus cervicis lateralis in *Desmognathus f. fuscus* showing the reduction of the omohyoideus.

FIG. 3. Characteristics of the m. rectus cervicis lateralis in *Eurycea l. longicauda* showing the reduction of the omohyoideus.

FIG. 4. Characteristics of the m. rectus cervicis lateralis in the genus *Pseudoeurycea* and the complete loss of the omohyoideus.

In summary, two points are evident: First, the omohyoideus is slowly reduced from *Desmognathus* through the more generalized plethodontids to *Eurycea* and finally is lost in the adults of the genera (*Pseudoeurycea* for example) considered in this study. Second, the lateral slip as seen in the Plethodontidae is distinct from the main body of the M. rectus cervicis superficialis, but since it is undoubtedly a specialized muscle derived from the rectus cervicis superficialis, it may be appropriately named the *rectus cervicis lateralis.*

*M. abdominohyoideus* (Smith 1920) (pl. LXVIII, fig. A).

The most striking and certainly the longest muscle in these salamanders is the abdominohyoideus. It arises on the medial and posterior margins of the ischiopubic plate and extends anteriorly along the lateral edge of the rectus abdominis and the posterior part of the rectus cervicis profundus. At approximately the level of the posterior tip of the thyroid gland, or slightly posterior in a few species, the abdominohyoideus curves medially deep to the rectus cervicis and often becomes convoluted or folded before passing ventrad to the second ceratobranchial and dorsad to the first ceratobranchial as the muscle extends anteriorly parallel to the elongate first basibranchial. The abdominohyoideus is inserted in a short tendon, which is in turn attached to the ventral surface of the tongue anterodorsal to the tip of the basibranchial. A ventral slip becomes separated from the main body of the muscle at, or a short distance anterior to, the level of the sternal cartilage and is inserted in the inscriptio tendinis.

The abdominohyoideus muscle is so uniform throughout all the genera studied that it is not included in the generic descriptions. The only important variations noted in this muscle were those associated with the level at which the ventral slip diverges from the main body of the muscle.

*M. subarcualis rectus I* (Edgeworth 1920).

This muscle has become specialized throughout the family and has reached a high degree of development in all Mexican and Central American plethodontids. The muscle arises on the ventral surface of the ceratohyal, beginning along the medial margin and extending across to the lateral edge approximately at the level of the anterior edge of the suprapeduncularis. It continues posteriorly along the lateral edge of the ceratohyal to a point near the level of the posterior tip of the mandible. The insertion is medially along the inscriptio tendinis and is laterally on the distal ends of the ceratobranchials and the tendinous sheath enclosing the epibranchial.

The size, particularly the length, is exceedingly variable among the genera and has been used as an important diagnostic character.

*M. suprapeduncularis* (Smith 1920).

The origin of the suprapeduncularis is on the dorsomedial surface of the ceratohyal a short distance posterior to its proximal end, and it is extended posteriorly for a short distance, usually for approximately the same length as the longest fibers of the muscle. The length and width as well as the shape of the muscle are variable, and there is always a characteristic "U" or "V" shaped indentation along the anterior margin of the muscle. The suprapeduncularis is distinct and is not in any way fused with the pharyngeal fibers of the throat area. In fact, there are few pharyngeal fibers in most genera that could in any way be confused with the posterior fibers of the suprapeduncularis muscle.

*M. hyoglossus* (Fischer 1843).

This muscle usually arises on the anterior end of the basibranchial between the cornua, and it inserts in the anterior semicircle of the tongue. Though I have not been able to observe the action of the tongues of these salamanders, the ventral position of the hyoglossus muscle suggests its obvious function; as the tongue is forced from the mouth the hyoglossus contracts to pull the dorsal horizontal surface to a vertical position and thus provides an efficient feeding apparatus. This is important because this surface of the tongue is richly supplied with a sticky mucous which is most essential in holding food items until they are pulled into the mouth.

## THE HYOBRANCHIAL SKELETON

The cartilaginous hyobranchial skeleton is composed of the elongate and rounded first basibranchial; two ceratohyals, which are flattened in the middle, attenuated and hooked on the distal end, and variously flattened or attenuated on the proximal end; a small round first ceratobranchial with the proximal end slightly flattened; and a larger round second ceratobranchial and a greatly elongated rod-shaped epibranchial, which articulates proximally with the distal ends of the ceratobranchials and usually extends to or posterior to the anterior edge of the front leg when the leg is at right angles to the body. The second basibranchial is missing in all genera and is represented by a vestige of connective tissue called the inscriptio tendinis. The lingual cartilage is also missing in all Mexican and Central American genera of Plethodontidae.

Certain statements made by Piatt (1935:228) are not entirely correct when representatives of all the Mexican and Central American plethodontids are carefully examined. First, the cornua on the anterior tip of the basibranchial are not "rather short" but are extremely short in *Thorius,* and are long and curved in some *Bolitoglossa.* Second, the ceratohyals are not "extremely slender" in most forms. The ceratohyals of typical *Oedipina* are the most slender of all examined, and since three of the five species seen by Piatt were of this genus, this may have been the influencing factor.

I have found the proximal third of the ceratohyals to vary sufficiently to allow use of the variation as reliable taxonomic characters. The ceratohyals are long and attenuated in the more specialized genera of *Thorius* and *Oedipina,* but with this difference: in *Thorius* the proximal ends of the ceratohyals are round and rodlike, whereas in *Oedipina* they are slightly flattened and are noticeably wider than thick. In *Bolitoglossa* and *Magnadigita* the ceratohyals are shorter and terminate in a bluntly rounded end with little or no flattening proximally. In the other genera (*Pseudoeurycea, Chiropterotriton, Lineatriton* and *Parvimolge*) the proximal end is lengthened and flattened in various ways depending on the genus. In *Pseudoeurycea* and *Parvimolge* the ceratohyal ends proximally in a nearly symmetrical lobe, but is not exactly spatulate; therefore, I have referred to this proximal lobe as a "spade" in these genera. In *Chiropterotriton* the anterior lobe is not symmetrical, and because it is more flattened medially than laterally, I have referred to it as a "bladelike" structure.

The middle part of the ceratohyal in all genera of Mexican and Central American plethodontids, save *Oedipina,* is broad, with a medial lobe extending nearly to the mid-line in some species.

The distal third of the ceratohyal is always slender, attenuated, and usually it has a sharp curve a short distance caudad to the posterior tip of the mandible. The distal end is always attached to the skull either directly or by a ligamentous sheath and is with few exceptions attached to the squamosal, although in some of the more primitive species it is difficult to determine whether it is attached to the quadrate or the squamosal, or whether it actually articulates with both. It is certainly not attached to the quadrate in all species as suggested by Cope (1889:120).

## ACKNOWLEDGMENTS

It has been possible to complete the present study only through the generosity and whole-hearted support of Dr. Edward H. Taylor, who has provided the greater part of the material and has extended invaluable courtesies and suggestions throughout the preparation of this paper. I am indebted also to Dr. A. B. Leonard and Dr. Charles D. Michener of the University of Kansas for their many helpful criticisms and suggestions; to Mr. Benjamin Shreve for the loan of specimens from the Museum of Comparative Zoology; to Mr. Harry C. Parker, who collected and sent specimens from Yosemite National Park; to Dr. Sherman A. Minton, Jr., Indiana University Medical Center, for many specimens; and to Dr. E. R. Hall and other staff members of the University of Kansas for aid and encouragement extended during the course of this work.

## DESCRIPTION OF THE THROAT MYOLOGY AND THE HYOBRANCHIAL CARTILAGES

### The Genus *Pseudoeurycea* Taylor

*Pseudoeurycea* Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, no. 12, 1944, p. 209 (type *Spelerpes leprosus* Cope).

The genus *Pseudoeurycea* includes a large assemblage of rather diverse but generalized terrestrial species. As a whole they are characterized by having the toes unwebbed beyond the metatarsals or metacarpals. In certain forms the webbing may extend on to the first phalanges of the outer fingers and toes but the middle digits are usually free. The distal phalanges are provided with rounded or ovate subterminal pads, while the palms and soles are smooth and unspecialized. There is a large sublingual fold present beneath the outer and anterior margins of the tongue. The species are moderate to large in size, in fact the largest plethodontid salamanders known, *P. bellii* and *P. gigantea,* belong to this genus.

The following muscle descriptions represent the general conditions obtaining in the genus. Any noteworthy departures from, or specializations of, the usual arrangement will be indicated.

#### TRANSVERSE THROAT MUSCLES

*M. intermandibularis anterior* (pl. LXVIII, fig. D; pl. LXIX, figs. B, C, & I).

The origin of this muscle is in fascia along the anterior margin of the anterior slip of the intermandibularis posterior. In all species the fascia extending laterad from the origin to the mandible becomes fused with the fascia on the anterior and dorsal surfaces of the anterior slip. There is no indication of a median raphe, except in *goebeli,* and *rex,* in which the posterior part of the muscle is divided at the mid-ventral line. It is doubtful whether this muscle is present in *cephalica cephalica* and *robertsi.* It was not present in the specimens that I examined. In *bellii* the males have this muscle well developed, whereas in the female it is present in only approximately half of the specimens examined and is in a much reduced condition when compared with the muscle in the males. This condition may exist in both *cephalica* and *robertsi* in which I have seen only female specimens. This muscle reaches its greatest size in *leprosa,* and is, with the lone exception of *robertsi,* well developed in all the species closely related to *leprosa* (*goebeli, rex, nigromaculata* and *cochranae*). There is less specialization of this muscle in *Pseudoeurycea* than in any of the genera studied save *Thorius* where it is totally absent.

*M. intermandibularis posterior* (pl. LXVIII, fig. D; pl. LXIX, figs. B, C, & I).

The anterior slip originates on the dorsomedial surface of the mandible approximately one third of the length of the mandible caudad to the symphysis. The insertion is in the ventral aponeurosis and anteriorly at the mid-ventral line. The proportion of fibers reaching the mid-line varies among the species. Approximately one fourth of the fibers reach the mid-line in *bellii* and *gadovii*, while in *rex* and *goebeli* only the most anterior fibers reach the mid-line.

The posterior slip originates on the dorsomedial surface of the mandible, beginning at a point 1 or 2 mm. anterior to its posterior tip and extending craniad for approximately one third the length of the mandible. The insertion is in the ventral aponeurosis, and with no fibers reaching the mid-ventral line, although they approach more closely this line in *Pseudoeurycea* than in any of the genera studied.

*M. gularis* (pl. LXVII, fig. D; pl. LXIX, figs. B, C, & I).

The origin of the anterior part arises in a thin sheet of fascia whereas the posterior part originates in the fascia cephalodorsalis. The fascia cephalodorsalis is a term used by Drüner to designate the fascia extending caudad from near the otic capsule to the gular fold, beneath the horizontal postocular skin groove and which lies immediately ventrolaterad to the dorsalis trunci muscles. Several muscles have part or all of their origin in this fascia. The thin fascia extending from the anterior part of the gularis is attached to the lateral edge of the mandible; to the quadrate; to the squamosal between the MM. depressor mandibulae and the capitis mandibularis, and to the lateral edge of the otic capsule. The thin fascia disappears shortly caudad to the skull. The insertion is on the skin of the gular fold and along the linea alba. The proportion of the muscle inserted at the linea alba is variable. In *bellii* and *gigantea* there is approximately one fourth of the total insertion at the linea alba while in *goebeli* there is less than one fifth of the muscle inserted here.

In *Pseudoeurycea* the gularis is large, both the origin and the insertion being extensive, and there is a large proportion of the muscle inserted at the linea alba.

*M. depressor mandibulae anterior.*

The anterior muscle originates chiefly on the dorsolateral surface of the squamosal and the lateral edge of the otic capsule. The fibers arising from the latter are usually deep to the cucularis major. In most species a few fibers arise from the posterior edge of the quadrate. The insertion is on the dorsal part of the posterior tip of the mandible.

*M. depressor mandibulae posterior.*

The posterior muscle originates in the fascia cephalodorsalis deep to the gularis but superior to the cucularis major. The insertion is on the posterior tip of the mandible ventral to the insertion of the anterior muscle.

The depressor mandibulae muscles are uniformly developed throughout the genus *Pseudoeurycea* with the exception of *robertsi.* In *robertsi* the division of the two muscles is not clearly marked and the dorsal part of the anterior muscle does not lie deep to the cucularis major.

*M. quadrato-pectoralis* (pl. LXVIII, fig. D; pl. LXIX, figs. B, C, & I).

The origin of the quadrato-pectoralis is variable. In most species the larger portion of this muscle is on the posterior surface of the dorsal end of the quadrate. In many other species a few fibers arise from the posteroventral edge of the squamosal and from the fascia surrounding the tip of the ceratohyal. In *gigantea, bellii* and *smithi* the origin is entirely on the quadrate, while in *cochranae* and *rex* it is mainly on the squamosal. The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis. The anterior fibers are inserted deep to the intermandibularis posterior except in *cochranae.*

The attachment of this muscle on the quadrate is another of the several primitive conditions existing in *Pseudoeurycea.* There appears to be a well-established phylogenetic relationship leading from the most primitive or generalized species, *bellii* and *gigantea,* through to the more specialized *cochranae* and *rex* of group III.

*M. interhyoideus* (pl. LXVIII, fig. D; pl. LXIX, figs. B, C, & I).

The origin of the interhyoideus is on the anteroventral surface of the anteriorly projecting distal end of the ceratohyal. The origin extends from a point near the attachment of the ceratohyal to the skull, caudoventrally to the lateral curve or hook of the ceratohyal posterior to the skull. The anterior fibers arise near the posterior fibers of the quadratopectoralis but there is a clear distinction between the origins of the two muscles. The insertion is in the ventral aponeurosis deep to the posterior slip of the intermandibularis posterior. The insertion is broad, extending almost to the anterior edge of the posterior slip.

### THE LONGITUDINAL AND DEEP MUSCLES

*M. geniohyoideus medialis* (pl. LXXI, figs. A, C, & E; pl. LXXIII, fig. H).

The origin of the medialis is on the posterior surface of the mandible lateral to the symphysis and always anterior to the origin of the anterior slip of the intermandibularis posterior. The insertion extends from the lateral edge of the subarcualis rectus 1 medially across its ventral surface and along the anterior edge of the inscriptio tendinis. The insertion extends medially to the mid-ventral line in *bellii, gigantea, leprosa* and *cephalica* and is partly or entirely posterior to a line between the posterior tips of the mandibles in all except *rex*. In this species the lateral part of the muscle extends only to the posterior tip while in *nigromaculata* the entire insertion is considerably anterior to such a line.

*M. geniohyoideus lateralis* (pl. LXXI, figs. A, C, & E; pl. LXXIII, fig. H).

The origin of the lateralis is on the posterior edge of the mandible dorsal and lateral to the medialis and anterior to the anterior slip of the intermandibularis posterior in all species. The medial half, or more, of this muscle arises dorsal to the medialis in all species except *nigromaculata* in which only a small fraction is dorsal. The insertion is on the lateral edge of the ceratohyal, beginning posterior to the caudal end of the mandible and extending anteriorly to near the middle of the cartilage. In *nigromaculata* the insertion is entirely anterior to the posterior tip of the jaw.

*M. rectus cervicis superficialis* (pl. LXXI, figs. A, C, & E).

The origin of this muscle is on the anterolateral edge of the sternum. In *bellii, gigantea, gadovii, unguidentis* and *cephalica* this muscle entends anteriorly and anterolateraly to cover the profundus muscle at the first myocomma anterior to the sternum. In the species of group III, the superficialis does not reach to the lateral edge of the profundus at the first myocomma, and there is a noticeable reduction in the size of the sternum and the relative width of the superficialis at its origin. In *smithi* the two muscles are not clearly separable into a superficialis and a profundus. In all species studied the superficialis is fused with the profundus anterior to the first myocomma and extends with it to a common insertion.

*M. rectus cervicis profundus* (pl. LXXI, figs. A, C, & E).

In *Pseudoeurycea* the profundus is almost entirely a continuation of the rectus abdominis muscles, with only a few fibers arising from the lateral edge of the sternum. In *gigantea* no fibers arise from the sternum or any of the lateral fascia attached to it. The insertion is on the medial part of the subarcualis rectus 1 and extends medially along the posterior edge of the inscriptio tendinis to the mid-ventral line.

The rectus cervicis is divided into three unequal segments by two myocommata. The posterior segment is approximately as long as the combined lengths of the two anterior segments, the middle segment being the shortest. From the medial part of the anterior myocomma deep to the main mass of the rectus cervicis is a small slip extending deep to the second ceratobranchial and inserted on the floor of the mouth a short distance posterior to the ceratohyals and suprapeduncularis. In *bellii* this slip inserts on the posterior edge of the ceratohyals immediately caudal and lateral to the posterior fibers of the suprapeduncularis, while in *gigantea* only a few lateral fibers reach the ceratohyals, the medial fibers being inserted on the floor of the mouth. In *bellii* and *gigantea* the muscle is also proportionally larger and wider than it is in other species. This size difference is particularly noticeable when compared with the species of group III.

*M. rectus cervicis lateralis* (pl. LXXI, figs. C, & E).

The origin of the lateralis is on the edge of the sternum immediately lateral to the rectus cervicis superficialis. From the origin it extends diagonally across the rectus cervicis profundus and anteriorly along the lateral surface of the abdominohyoideus approximately to the level of the thyroid gland where it is inserted in fascia. It has been difficult to determine accurately the insertion, chiefly because of the small size of the muscle and also owing to a peculiar branching of the fibers at or just before the insertion.

*M. subarcualis rectus 1* (pl. LXXI, fig. A; pl. LXXII, fig. F; pl. LXXIII, figs. B, E & H; pl. LXXIV, fig. C).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning at the base of the anterior ovate "spade" of the ceratohyal and extending caudad along the lateral edge of the ceratohyal to a point beyond the posterior tip of the mandible. A smaller part extends caudad along the medial edge of the ceratohyal approximately to the posterior edge of the suprapeduncularis. In *nigromaculata* and *rex* the posterior fibers are attached to the mandible a short distance anterior to its posterior tip. The insertion extends along the anterior edge of the inscriptio tendinis to the distal ends of the ceratobranchials and in the tendinous sheath of the epibranchial. The insertion extends medially to, or nearly to, the mid-ventral line. The muscle is noticeably elongate and extends well beyond the posterior level of the insertion of the arm in all species.

*M. suprapeduncularis* (pl. LXXII, fig. F; pl. LXXIII, figs. B, E & H; pl. LXXIV, fig. C).

This muscle arises on the dorsomedial surface of each ceratohyal and extends transversely dorsal to the tongue stalk. In *Pseudoeurycea* the suprapeduncularis is well developed and is easily distinguished from any other tissues in the pharyngeal region of the mouth. The anterior fibers are longest and are curved caudomedially to produce a U-shaped anterior border. The fibers become progressively shorter and more transverse caudad. The muscle extends from the base of the expanded anterior "spade" of the ceratohyals posteriorly for a distance approximately equal to the length of the fibers or, as in *nigromaculata*, until the medial lobes of the ceratohyals are almost approximating each other immediately posterior to the muscle. In *nigromaculata* and *rex* the ceratohyals are rather close together and the suprapeduncularis appears as a wide, greatly shortened muscle.

*M. hyoglossus.*

The origin of the hyoglossus is on the anterior tip of the basibranchial between the cornua. The insertion is in the tongue tissue anterodorsal to the origin. This is a well-formed, narrow muscle, several fibers thick at the origin and fanning out into a thin broad muscle at the insertion.

In *Pseudoeurycea* the ceratohyals are elongate, attenuated posteriorly and, with the exception of *nigromaculata*, curved at less than a right angle posterior to the caudal end of the mandible. The anterior end is expanded into a broad flattended spade, the medial edges of which extend nearly to the mid-ventral line. In *nigromaculata* the entire anterior half of each ceratohyal is expanded into a more flattened and broader spadelike structure than is to be seen in other species of the genus. Furthermore, in *nigromaculata* the ceratohyals extend to the posterior edge of the mandible near the symphysis, a condition most unusual in this genus.

## Summary

On the basis of the throat myology and the structure of the ceratohyals it is possible to arrange the species of *Pseudoeurycea* into the following three groups:

Group I
*bellii*
*gigantea*
*smithi*
Group II
*gadovii*
*unguidentis*
*cephalica*
Group III
*leprosa*
*robertsi*
*cochranae*
*goebeli*
*rex*
*nigromaculata*

The species of group I are apparently the most generalized of the genus. The origin of the quadrato-pectoralis on the quadrate, the broad insertion of the anterior slip of the intermandibularis posterior, the insertion of the gularis at the mid-ventral line and the relatively large rectus cervicis lateralis are all primitive characters. A consideration of each character separately may make it possible to point out more clearly the reasons for such conclusions.

In the more generalized genera of the family Plethodontidae, *Plethodon* for example, the quadrato-pectoralis arises from the posterior edge of the dorsal tip of the quadrate and the ligamentous tissue surrounding the tip of the ceratohyal. Furthermore, a line of distinction is not apparent between the quadrato-pectoralis and the interhyoideus, especially at their origin along the distal end of the ceratohyal and the quadrate. The two muscles are separate in both *bellii* and *gigantea,* but the quadrato-pectoralis has continued to maintain a primitive origin.

I have come to regard broad insertions at the mid-ventral line as primitive, mainly because of the broad insertions found in Salamandridae, a family known to be more primitive than Plethodontidae and considered by many to be the ancestral stock from which the Plethodontidae arose. In the larvae of the Salamandridae, and in the Ambystomidae, all of the superficial transverse throat muscles are inserted at the median raphe. If such a condition existed in the ancestral stock, then the extent of departure from such a pattern would indicate the degree of primitiveness in more specialized species. There is a possibility of a secondary specialization, but I can see no reason for considering such a possibility when other factors point to an obviously primitive condition.

The rectus cervicis lateralis reaches a greater degree of development in *Pseudoeurycea* than in any of the genera considered herein. It is a large muscle and is easily traced from the origin to the insertion, especially in the larger species. In *smithi* the rectus cervicis lateralis is small, approximately one third the size of that obtaining in a specimen of *bellii* of the same length. Except for this one character, *smithi* is much the same as *bellii,* to which it appears to be most closely related.

The species of group II are also rather primitive and are, on the basis of myology, more closely related to group I than to group III. In these species the origin of the quadrato-pectoralis is principally on the quadrate, but with a few posterior fibers arising from the squamosal. The rectus cervicis lateralis is small, but the insertion of the transverse muscles along the mid-ventral line is broad.

Group III represents the most specialized species in the genus *Pseudoeurycea.* Except for *robertsi,* the intermandibularis anterior is present and larger than in the species of group II. In *gigantea* and in the males of *bellii* this muscle is approximately the same relative size as it is in the species of group III. In *leprosa* and *nigromaculata* the anterior muscle has become triangular in shape and is strikingly similar to that found in *Chiropterotriton multidentata* and *C. terrestris.* It appears to be a result of an adaptation to similar environmental situations.

In group III the origin of the quadrato-pectoralis is almost equally divided between the quadrate and the squamosal. In *leprosa* and *goebeli* a larger part arises from the quadrate, whereas in *cochranae* and *rex* almost the entire muscle originates on the squamosal. The insertions at the median raphè are narrower, and the rectus cervicis lateralis is very small (largest in *leprosa*).

A further difference between the groups is the length of the posterior segment of the rectus cervicis in proportion to the rest of the muscle. In group III the posterior segment is, save for *nigromaculata,* always less than half the length of the entire muscle. In the other groups the posterior segment is approximately half, or as in *smithi* noticeably more than half, the length of the entire muscle.

The two most divergent species in group III are *nigromaculata* and *robertsi.* The species *leprosa, goebeli,* and *cochranae* are the most closely related in the group. In *rex* and *goebeli* a division of the posterior half of the intermandibularis anterior at the median raphe has led me to suspect that the absence of this muscle in *robertsi* is more apparent than real, and it is actually completely divided and fused with the anterior slip of the intermandibularis posterior. It is possible that an examination of a series of individuals of this species would reveal some specimens with the muscle developed. At present I can offer no explanation for the unusual divergence existing in *nigromaculata.*

## The GENUS *Chiropterotriton* Taylor

*Chiropterotriton* Taylor, Univ. Kansas Sci. Bull., vol. 30, no. 12, 1944, p. 213 (type *Oedipus multidentatus* Taylor).

This genus includes, at present, twelve species of small terrestrial and arboreal salamanders. The digits of hand and foot are widely spread, usually truncate, and bear small subdigital pads under the terminal phalanges. The proximal phalanges and the entire first finger and toe are included in the smooth pad of the palm and sole. In the young of all species and in the adults of *dimidiata, nasalis* and *bromeliacea,* the nostrils are very much enlarged. The carpals and tarsals are cartilaginous and there is a distinct sublingual fold below the anterior part of the free tongue.

The muscles and muscle patterns show specializations not seen in other Mexican and Central American genera. The intermandibularis anterior and hyoglossus are proportionally larger and more specialized than in other genera. The extent of these and other modifications will be indicated as the individual muscles are described.

### TRANSVERSE THROAT MUSCLES

*M. intermandibularis anterior* (pl. LXVIII, fig. A; pl. LXIX, figs. A, D, G, H & J).

The origin of the muscle is in a small narrow strip of fascia, deep to the anterior slip of the intermandibularis posterior. The fascia extends laterally to attach to the dorsomedial surface of the mandible together with the fibers of the anterior slip of the posterior muscle. The shape of the muscle varies among the several species. In *multidentata, terrestris, dimidiata,* and *xolocalcae* it is triangular with the median angle extending as a wedge between the two opposing slips of the intermandibularis posterior; the anterior edge of the muscle is only slightly convex, in fact it is nearly transverse. In *arborea, nasalis, chiroptera, chondrostega,* and *lavae,* the muscle is expanded at the mid-ventral line but does assume a triangular shape. In this latter group the anterior edge of the muscle may vary from concave as observed in *chondrostega* to convex in *chiroptera*. More important is its relatively large size in this genus. In typical *Chiropterotriton* this muscle reaches perhaps a higher state of development than in any genus in the family Plethodontidae.

In *abscondens*, the intermandibularis anterior has been completely lost. Because of this loss and other rather different variations to be considered later I have come to consider *abscondens* as an atypical species, which is myologically rather widely separated from the more typical forms of the genus.

*M. intermandibularis posterior* (pl. LXVIII, fig. A; pl. LXIX, figs. A, D, G, H, J & K).

The *anterior slip* originates along the dorsomedial surface of the mandible and the anterior margin is approximately one third of the length of the mandible posterior to the symphysis. The width of the origin varies from .3 to 1 mm, within the genus depending on the size of the individuals which make up the species. In *abscondens* the origin is .6 mm wide and is proportionally wider than in specimens of *terrestris, lavae, chondrostega* and *xolocalcae*, all of which have approximately the same snout to vent lengths (25-28 mm) and in which this muscle has a width at the origin of only .45 to .5 mm.

The muscle extends fanwise to the insertion in the ventral fascia with the most anterior fibers reaching the mid-ventral line, except in *abscondens* where they are just short of the line.

In all species, except *abscondens*, the anterior fibers extend from the origin to the insertion in a caudomedial direction. In *abscondens* the anterior fibers extend in an anteromedial direction and have come to occupy much of the area taken up by the anterior muscle in other species. This apparent anterior shift may serve to compensate for the loss of the intermandibularis anterior. Obviously the shift has increased the size of the muscle and, as in the case of its origin, substantially increased the proportional width of the insertion, when compared with other species. The slip in *abscondens* is therefore a much different muscle than it is in other *Chiropterotriton*.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible. The insertion is a broad fan in the ventral aponeurosis, between the anterior slip and the quadratopectoralis muscle. None of the fibers reach the mid-ventral line.

In *abscondens*, the fibers are relatively shorter and the line of insertion is longer than in other species.

*M. gularis* (pl. LXIX, figs. A, D, G, H, J & K).

The origin of this muscle is entirely in fascia. Approximately the anterior half arises from a thin aponeurosis, which is attached to the lateral edge of the mandible, to the quadrate and squamosal between the MM. depressor mandibulae and capiti mandibularis, to the caudolateral edge of the otic capsule and caudally along the fascia cephalodorsalis. In *abscondens* and *nasalis* the aponeurosis is attached high on the quadrate and is not attached to the mandible. In the two latter species the gularis is posterior to the tip of the mandible exposing clearly the entire insertion of the depressor mandibulae. In *xolocalcae* and *multidentata* the ventral portion of the insertion of the depressor mandibulae is exposed but in these forms it is not clearly shown. The insertion of the gularis is primarily on the skin of the gular fold. In all species there are a few anterior fibers inserted along the linea alba.

*M. depressor mandibulae anterior* (pl. LXIX, figs. A, G & K).

The anterior muscle originates chiefly on the squamosal and the lateral edge of the otic capsule. In a few species, *xolocalcae* for example, the most anterior fibers arise from the posterior edge of the quadrate. The most dorsal (otic) part is always deep to the cucularis major. The insertion is on the dorsal surface of the posterior tip of the mandible.

*M. depressor mandibulae posterior* (pl. LXIX, fig. K).

The posterior muscle originates in the fascia cephalordorsalis deep to the posterior part of the gularis. The insertion is on the ventral surface of the posterior tip of the mandible.

*M. quadrato-pectoralis* (pl. LXIX, figs. A, D, G, H, J & K).

The origin of the muscle is usually on the posterior edge of the quadrate and the squamosal. The large part is attached to the squamosal, in *xolocalcae*, *dimidiata* and *abscondens*. In the latter three species I could find no fibers arising from the quadrate. In *abscondens*, the origin is definitely attached only to the squamosal. The insertion is in the ventral aponeurosis between the intermandibularis and the gularis. None of the fibers reach the mid-ventral line although in *abscondens* the posterior ones are just short of reaching the gular fold. In all species, except *abscondens*, the insertion of the most anterior fibers is deep to the intermandibularis posterior.

*M. interhyoideus* (pl. LXIX, figs. A, D, H & K).

The origin of the muscle is on the anteroventral edge of the ceratohyal approximately midway between its attachment on the squamosal and its sharp curve posterior to the tip of the articulare. The origin is clearly separated from the quadrato-pectoralis in all species. The insertion is in the ventral fascia deep to the anterior edge of the quadrato-pectoralis and the posterior part of the intermandibularis posterior. In *arborea, terrestris,* and *chiroptera* the insertion is entirely dorsal to the intermandibularis.

### THE LONGITUDINAL AND DEEP MUSCLES

*M. geniohyoideus medialis* (pl. LXVIII, fig. A; pl. LXIX, figs. G, J & K; pl. LXXI, fig. D).

The origin of this muscle is on the posterior surface of the mandible immediately lateral to the symphysis. The width of the origin varies between .4 and .7 mm. The insertion is on the ventral surface of the subarcualis rectus 1 and along the anterior edge of the inscriptio tendinis but not extending to the mid-ventral line. The insertion is proportionally narrowest in *multidentata* and widest in *chondrostega* and *chiroptera.* In all species the lateral part of the muscle inserts caudal to the posterior tip of the mandible.

*M. geniohyoideus lateralis* (pl. LXVIII, figs. A & B; pl. LXIX, figs. G, J & K; pl. LXXI, fig. D).

The origin of the muscle is on the posterior and medial surfaces of the mandible, lateral to the medialis, except in *nasalis,* in which the medial fibers are dorsal to the medialis. In *arborea, xolocalcae, nasalis* and *abscondens* this muscle is divided near its origin by the anterior slip of the intermandibularis posterior and the intermandibularis anterior and there is a short distance between the two parts. In these species the largest part of the muscle arises on the medial edge of the mandible posterior to the anterior slip of intermandibularis posterior. In *dimidiata, chondrostega, lavae* and *multidentata* a few of the lateral fibers arise from fascia on the floor of the mouth immediately mediad and caudad to the origin of the anterior slip of the intermandibularis posterior. In *lavae* the fibers extend almost to the mandible.

The insertion is on the lateral edge of the ceratohyal, beginning medial to the posterior tip of the mandible, or slightly posterior to it in some species, and extending anteriorly approximately to the middle of the ceratohyal.

There appears to be a correlation between the extent of the development in the length of the origin of this muscle and the degree to which the species have attained aboreal habits. In *chiroptera* and *terrestris,* two entirely terrestrial species, the origin is completely anterior to the origin of the anterior slip of the intermandibularis posterior. An intermediate group composed of *dimidiata, chondrostega* and *multidentata* have the lateral fibers arising in fascia posterior to the mandible and medial to the origin of the intermandibularis muscles. These species are, according to the few sketchy reports dealing with them, mainly terrestrial. The species *lavae* can best be considered alone since it is mainly arboreal and has the origin of the lateral fibers reaching nearly to the mandible posterior to the intermandibularis. In the wholly arboreal species, (*arborea, xolocolcae* and *nasalis*) this muscle attains its greatest extent of attachment with approximately two thirds of the muscle arising on the mandible posterior to the anterior slip of the intermandibularis posterior. I have not seen *bromeliacia* but since it is entirely arboreal and closely related to *nasalis* (Schmidt 1936), I suspect that as regards this character, it will be the same as in *nasalis.* The habits of *abscondens* are not fully known. The few specimens collected were found under the bark of old stumps. The muscle arrangement and the attachment to the mandible in *abscondens* is similar to that in arboreal species, except that the part of the muscle arising posterior to the anterior slip represents only approximately half instead of two thirds of the origin.

*M. rectus cervicis superficialis* (pl. LXVIII, fig. A; pl. LXXI, fig. D).

The origin of the muscle is on the anterolateral edge of the sternum in all species. The fibers extend anteriorly and anterolaterally to cover completely the profundus at the first myocomma. From this point anteriorly the muscle is inseparably fused with the profundus. The insertion is with the profundus and will be described with the insertion of the following muscle.

*M. rectus cervicis profundus* (pl. LXVIII, fig. A; pl. LXXI, fig. D).

The major portion of this muscle is a direct continuation of the rectus abdominis. A small medial part arises from the lateral and anterolateral edge of the sternum, the more medial of which are deep to the superficialis. The insertion begins on the median surface of the subarcualis rectus 1 and extends medially along the inscriptio tendinis to the mid-ventral line. The insertion is in an irregular diagonal line.

The muscle is composed of three segments of unequal length; the posterior segment is approximately as long as the combined length of the other two; the middle segment is the shortest. The medial fourth of the anterior segment extends deep to insert on the floor of the mouth a short distance posterior to the suprapeduncularis. In *Chiropterotriton* this slip is narrow and the fibers converge at the insertion.

*M. rectus cervicis lateralis* (as in pl. LXXI, figs. C & E).

The origin of this muscle is on the lateral edge of the sternum or on the myocomma immediately lateral to the sternum. The Insertion is in fascia which is on the lateral surface of the abdominohyoideus at approximately the level of the thyroid gland.

This muscle occurs in all species, except *nasalis* where it is apparently not present, at least not in the single specimen examined. It is an extremely small muscle throughout the entire genus, reaching its largest size in *chiroptera.* It was readily discernible in the very small *dimidiata.*

*M. subarcualis rectus* 1 (pl. LXVIII, fig. A; pl. LXXI, fig. D; pl. LXXIII, fig. C).

The origin of the muscle is on the ventral surface of the ceratohyal, beginning at the base of its anterior blade and extending caudad along its lateral edge to a point medial to the posterior tip of the mandible or slightly posterior in some species. A shorter row of fibers arises along the medial edge of the ceratohyal. The insertion begins near the mid-ventral line and extends laterally along the inscriptio tendinis to the distal ends of the ceratobranchials and the tendinous sheath surrounding the epibranchial. The muscle extends caudally at least to the posterior margin of the front leg in all species. It is proportionally shortest in *chondrostega* and longest in *xolocalcae.* In *nasalis, arborea, multidentata* and *abscondens* it is relatively elongate.

*M. suprapeduncularis* (pl. LXVIII, fig. B; pl. LXXIII, fig. C).

This muscle is attached to the dorsomedial surface of the ceratohyals beginning at the base of the anterior blade and extending caudad to the point at which the ceratohyals curve laterad. There are no transverse pharyngeal fibers posterior to it, except in *abscondens.* In this genus the suprapeduncularis is relatively uniform in size and shape.

*M. hyoglossus* (pl. LXVIII, fig. C).

The muscle arises on the ventral surface of the anterior tip of the basibranchial. From the origin the fibers extend fanwise anterodorsally to insert in the tissue of the tongue.

The ventral origin of the hyoglossus is peculiar to the genus *Chiropterotriton* and may be used as a reliable generic character.

In the genus *Chiropterotriton* the anterior part of the ceratohyal is curved ventrally around the stalk of the tongue and terminates anterior to the suprapeduncularis in a narrow blade. The thin medial edges of the two opposing "blades" are almost in contact at the linea alba. The exception to this is in *abscondens,* in which the ceratohyal terminates in a round attenuated rod of cartilage, with no suggestion of a flattening of the proximal ends.

## Summary

The genus *Chiropterotriton* has undergone adaptive specializations to such an extent that it is now possible, on the basis of the throat myology and the nature of the ceratohyals, to arrange the species into three groups. The groups are not of equal taxonomic value and are established for the express purpose of indicating the specific and intra-specific variations extant in the genus.

Group I
- *chiroptera*
- *terrestris*
- *chondrostega*
- *dimidiata*
- *multidentata*
- *lavae*
- (*mosaueri*)

Group II
- *arborea*
- *xolocalcae*
- *nasalis*
- (*bromeliacia*)

Group III
- *abscondens*

Species in parenthesis were not seen, and their position is tentative.

The species of group I are, on the basis of muscle patterns, the most generalized of the genus. The geniohyoideus has not become specialized, and the subarcualis rectus 1 is relatively shorter than in either of the other groups. The muscles appear to be least specialized in *chiroptera* and *chondrostega* and most specialized in *lavae.* The most generalized form in this group appears to be *chiroptera,* which may represent the nearest link to the ancestor of the genus. I am inclined toward the opinion that the ancestors of these salamanders were entirely terrestrial in their habits.

In group II the species are entirely arboreal in habit, and all have a highly specialized geniohyoideus lateralis and a much longer subarcualis rectus 1. The real reason for these specializations is unknown to me, but I suspect them to be correlated with changes in feeding habits and possibly with their behavior associated with climbing. Aside from these differences, the species of group I and II are similar and together form a closely related series of species developed as a result of adaptive radiation.

The single species in group III is more closely related to the aboreal species of group II than to those group I. This relationship does not appear to be close, however, for I can recognize no close relatives among the assemblage of known species. It should be pointed out, however, that *abscondens,* in spite of its attenuated ceratohyals and missing intermandibularis anterior, is not an annectant form relating, for example, *Thorius* with *Chiropterotriton.* The muscle patterns, unquestionably those of a *Chiropterotriton,* have been modified from the general muscle patterns of the genus, because of specializations brought about by its changing habits, habitats, or more probably both. The entire external anatomy, the shape of the feet and the hands, the dental patterns, the shape of the snout, and the absence of an orbitolabial groove all testify to its proper association with *Chiropterotriton.*

### GENUS *Parvimolge* Taylor

*Parvimolge* Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, no. 12, 1944, p. 223 (type *Oedipus townsendi* Dunn).

The genus *Parvimolge* includes only two known species of diminutive terrestrial salamanders. *P. townsendi* inhabits parts of Central Mexico while *P. richardi* is known only from Costa Rica. The following characteristics will distinguish them from any other Mexican or Central American salamanders. The middle digits are only approximately half webbed, with the distal half of each free and with the tips pointed. The middle toe and second finger are considerably longer than other adjoining digits. There is a sublingual fold present and the maxillary is toothed. The skull is well ossified; the carpals and tarsals are cartilaginous and the nasals are enlarged.

The following descriptions of the throat musculature and the hyobranchial cartilages will indicate certain of the anatomical conditions existing in this genus and will add to the known list of distinguishing characteristics.

The descriptions are based entirely on the throat anatomy of *townsendi,* except for a few characters which could be noted without dissecting the type specimen of *richardi.*

#### THE THROAT MYOLOGY AND THE HYOBRANCHIAL APPARATUS

#### TRANSVERSE THROAT MUSCLES

*M. intermandibularis anterior* (pl. LXIX, fig. F).

The origin of the anterior muscle is in fascia deep to the anterior margin of the anterior slip of the intermandibularis posterior. The fascia extends lateral in conjunction with that of the anterior slip and is attached to the dorsomedial surface of the mandible. The muscle is narrow, approximately .2 mm wide at the mid-ventral line and is .3 mm posterior to the symphysis. There is no sign of a median raphe.

*M. intermandibularis posterior* (pl. LXIX, fig. F).

The *anterior slip* originates on the dorsomedial surface of the mandible approximately .9 mm caudolateral to the symphysis. The insertion is in the ventral aponeurosis and anteriorly along the mid-ventral line. The latter represents about one fourth of the slip.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible. The insertion is in the ventral fascia. The median fibers are longest but do not extend to the mid-line.

Both slips have extensive insertions and are broadly fan-shaped, together they cover most of the area between the mandibles.

*M. gularis* (pl. LXIX, fig. F).

The origin of the gularis is in fascia; the anterior part arises from a thin sheet of fascia which is attached to the lateral surface of the posterior tip of the mandible, the quadrate, the squamosal and the otic capsule; the posterior part arises in the fascia cephalodorsalis. The insertion is on the gular fold except for a small anterior portion which inserts along the mid-ventral line. The posterior tip of the mandible is deep to this muscle.

*M. depressor mandibulae anterior.*

The anterior muscle arises from the squamosal and the otic capsule. The M. cucularis major arises from the skull along the caudal and dorsal edges of this muscle, and is not superior to the otic part of the depressor mandibulae as it is in most other genera. The insertion is on the dorsal surface of the posterior tip of the mandible.

*M. depressor mandibulae posterior.*

The posterior muscle arises along the fascia cephalodorsalis deep to the gularis and superior to the cucularis. The origin is extensive and reaches the gular fold. The insertion is ventral to the anterior muscle. Both muscles are large and distinctly separated.

*M. quadrato-pectoralis* (pl. LXIX, fig. F).

The origin of this muscle is on the posterior edge of the squamosal and on the ventral edge of the ligament attaching the ceratohyal to the squamosal. There are no fibers attached to the quadrate in the specimen examined. The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis.

*M. interhyoideus.*

The origin of the interhyoideus is on the anteroventral surface of the distal end of the ceratohyal. The insertion is in the ventral aponeurosis, deep to the intermandibularis posterior and the quadrato pectoralis. The larger part, comprising approximately two-thirds of the muscle, is deep to the intermandibularis.

### THE LONGITUDINAL AND DEEP MUSCLES

*M. geniohyoideus medialis* (pl. LXX, fig. E; pl. LXXII, fig. E). The origin of the medialis is on the posterior surface of the mandible beginning at the symphysis and extending laterad for approximately .4 mm. The lateral part of the muscle inserts on the ventral surface of the subarcualis rectus 1. The medial part is attached to the anterior edge of the inscriptio tendinis, but does not extend to the mid-ventral line. The insertion forms a diagonal line, with the lateral portion extending posteriorly to a line between the caudal tips of the mandible. The muscle is rather uniform in width and is only slightly wider near the insertion than at the origin.

*M. geniohyoideus lateralis* (pl. LXX, fig. E; pl. LXXII, fig. E). The origin of the lateralis is on the posterior surface of the mandible lateral and dorsal to the medialis. The origin of the lateralis does not extend to the anterior slip of the intermandibularis posterior, and there are no fibers arising in fascia laterad or caudad to the anterior slip. The insertion is on the lateral edge of the ceratohyal beginning approximately at the level of the posterior tip of the jaw and extending anteriorly for about .9 mm.

*M. rectus cervicis superficialis* (pl. LXX, fig. E; pl. LXXII, fig. E). The origin of this muscle is on the anterolateral edge of the sternum. The lateral edge of the origin is approximately half way between the mid-line and the lateral edge of the profundus. The superficialis does not reach to the lateral edge of the profundus at the first myocomma anterior to the sternum, but is closely applied to the profundus anterior to the first myocomma. The insertion is with the profundus.

*M. rectus cervicis profundus* (pl. LXX, fig. E; pl. LXXII, fig. E). The major portion of this muscle is a direct continuation of the rectus abdominis. A small medial portion arises from the sternum lateral and dorsal to the superficialis. The insertion is on the ventral surface of the subarcualis rectus 1, directly caudad to the geniohyoideus medialis, and extends medially along the inscriptio tendinis to the mid-ventral line. The posterior segment is approximately as long as the combined length of the two anterior segments; the most anterior segment is the shortest. The deep slip of the rectus cervicis is attached to the medial part of the anterior myocomma and is entirely deep to the superficial part of the muscle. This slip is inserted on the floor of the mouth posterior to the suprapeduncularis.

*M. rectus cervicis lateralis* (as in pl. LXXI).

The lateralis is present as a very fine bundle of fibers arising from near the extreme lateral edge of the sternum and extending anterolaterad to the lateral surface of the abdominohyoideus. How far it extended anteriorly could not be determined.

*M. subarcualis rectus 1* (pl. LXX, fig. E; pl. LXXII, fig. E).

The origin of this muscle is on the ventrolateral and ventromedial edges of the ceratohyal. The lateral part begins with the medial part at the base of the anterior "spade" of the ceratohyal, and extends posteriorly approximately to the level of the caudal tip of the mandible, whereas the medial part extends for only about half that distance along the medial surface. The insertion extends along the inscriptio tendinis, to the distal ends of the ceratobranchials and extends posteriorly along the tendinous sheath surrounding the epibranchial.

The muscle is proportionally longer in both species of *Parvimolge* than it is in any species of *Chiropterotriton* save *C. xolocalcae* in which it is approximately of the same relative length.

*M. suprapeduncularis* (pl. LXX, fig. E).

The origin of the suprapeduncularis is on the dorsomedial surface of the ceratohyals, beginning at the base of the enlarged anterior spade of the ceratohyal, which is approximately .4 mm from the anterior end, and extending caudad for about .5 mm. The anterior fibers are approximately a third longer than those near the posterior end. The muscle is widely separated from the deep slips of the rectus cervicis. The muscle resembles very closely that found in the genus *Chiropterotriton* and some *Pseudoeurycea*.

*M. hyoglossus.*

The origin of the hyoglossus is on the anterior edge of the basibranchial between the short anterolaterally projecting cornua. The insertion is in the anterior semicircle of the tongue anterodorsal to the origin.

The ceratohyals are similar in shape and size to those found in *Chiropterotriton* and *Pseudoeurycea*. They are peculiar in that the anterior lobes are considerably overlapped along the mid-ventral line and the medial lobes are widely separated. The other hyobranchial cartilages are not variable.

## GENUS *Magnadigita* Taylor

*Magnadigita* Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, 1944, pp. 189-232 (type *nigroflavescens*).

The genus *Magnadigita* includes at least fifteen species of medium to large terrestrial and arboreal salamanders. They range over the greater part of Central America and have entered southern Mexico and northern South America. The members of this genus are readily distinguished from all other genera by the complete absence of the sublingual fold and by having the tips of the digits truncate and the distal part of the digits free from webbing. This combination of characters is singular to the genus *Magnadigita* and together may be used as an easy method of recognizing the species of the genus. The habitats of the several species are rather variable, some being found in and under old logs, others in bromelias and some living under rocks and in live moss. The genus *Magnadigita* has seemingly undergone adaptive radiation in much the same way as have other large genera such as *Pseudoeurycea* and *Chiropterotriton* with the resulting large series of distinct and diversified species.

The following myological descriptions will indicate other less obvious characteristics of the genus.

### THE THROAT MYOLOGY AND THE HYOBRANCHIAL APPARATUS

### TRANSVERSE THROAT MUSCLES

*M. intermandibularis anterior* (pl. LXX, fig. C).

The origin of the anterior muscle is in fascia at the anterior edge of the anterior slip of the intermandibularis posterior. The medial and posterior fibers arise deep to the anterior slip. This muscle is absent in *robusta* and *subpalmata.* In *engelhardti* and *dunni* the muscle is very narrow being less than .2 mm wide in *engelhardti;* it is widest in *franklini* (.4 mm) and is well developed in *rostrata* and *macrinii.* This muscle is noticeably shorter than it is in other genera, having in *dunni,* a length of scarcely more than 1 mm. In *nigroflavescens* this muscle is inserted at the median raphe there being no fibers which are continuous across the mid-ventral line.

In *nigroflavescens* this muscle is completely divided and is inserted in fascia at or lateral to the mid-ventral line. Besides the variable sizes and conditions existing in this muscle, is the fact that in all species it is relatively small in size.

*M. intermandibularis posterior* (pl. LXX, figs. B & C).

The *anterior slip* originates on the dorsomedial surface of the mandible, approximately one third of the length of the mandible posterior to the mental symphysis. The insertion is in the ventral aponeurosis caudomedial to the origin. In *subpalmata, franklini* and *macrinii* the most anterior fibers reach the mid-ventral line, in all others the insertion is lateral to the mid-line. In some species approximately one third or more of the muscle arises from fascia extending from the mandible mediad along the edge of the anterior slip.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible. The insertion is in the ventral aponeurosis between the anterior slip and the quadrato-pectoralis. The posterior fibers are inserted anterior to a line between the posterior tips of the mandibles and there is a greater distance from the tip of the mandible to the origin of the most caudad fibers, than is commonly found in other genera.

*M. gularis* (pl. LXX, figs. B & C; pl. LXXII, fig. G).

The origin of the gularis is in a thin sheet of fascia, which is attached to the mandible and dorsad along the quadrate and squamosal to the lateral edge of the otic capsule. Posterior to the otic capsule the fibers arise directly from the fascia cephalodorsalis, thus eliminating the aponeurosis. A few of the superficial fibers arise from the skin. The insertion is on the skin of the gular fold and medially along the linea alba. A few of the anterior fibers of the muscle are inserted at the mid-ventral line, except in *robusta,* and the posterior tip of the mandible is always deep to the anterior edge of this muscle.

*M. depressor mandibulae anterior.*

The anterior muscle originates on the squamosal and the lateral edge of the otic capsule. Only the posterior fibers of the muscle arise from the otic capsule and these are deep to the cucularis major in all species except *robusta.* The insertion is on the dorsal surface of the posterior tip of the mandible.

*M. depressor mandibulae posterior.*

The posterior muscle originates in the fascia cephalodorsalis deep to the gularis. It does not extend caudad to the gular fold and is approximately the same size as that of the anterior muscle. The insertion is ventral to the insertion of the anterior muscle.

*M. quadrato-pectoralis* (pl. LXX, figs. B & C).

The origin of this muscle in *Magnadigita* is rather irregular and cannot be described in a single statement. In *macrinii, franklini, engelhardti* and *subpalmata* this muscle arises from the squamosal and the tendinous tissue attaching the ceratohyal to the skull. In other species the fibers arise from the quadrate, squamosal and from the tendinous tissue, although the proportions of origin vary considerably with most of the fibers arising from the squamosal in *rostrata* and with a greater part originating on the quadrate in *robusta*. The origin appears to be determined, in part at least, by the point of attachment of the ceratohyal on the squamosal, at least on the relative distance from the attachment to the dorsal tip of the quadrate. If the ceratohyal is attached near the dorsal tip of the quadrate and the most caudoventral edge of the squamosal, as in *robusta,* then much of the muscle arises from the quadrate. The origin is always in the angle between the ceratohyal and the skull, with at least one fourth of the muscle arising from the tendinous tissue around the ceratohyal and with the remainder arising from either the squamosal or from both the squamosal and the quadrate.

The insertion is in the ventral aponeurosis, the anterior fibers are deep to the intermandibularis posterior and in *robusta* and *macrinii* the posterior fibers extend to the gular fold and at that point reach the linea alba.

*M. interhyoideus* (pl. LXX; figs. B & C).

The origin of the interhyoideus is on the anteroventral surface of the ceratohyal between the outer edge of the curve in the ceratohyal caudad to the posterior tip of the jaw and its attachment to the squamosal. The insertion is in the ventral aponeurosis deep to the posterior slip of the intermandibularis posterior. In *robusta* and *nigroflavescens* the posterior part of this muscle is deep to the quadrato-pectoralis.

### THE LONGITUDINAL AND DEEP MUSCLES

*M. geniohyoideus medialis* (pl. LXXIV, fig. E).

The origin of the medialis is on the posterior margin of the mandible, beginning at the symphysis and extending laterad for more than half the distance from the symphysis to the origin of the anterior slip of the intermandibularis posterior. The insertion is on the ventral surface of the subarcualis rectus 1 and medially along the anterior edge of the inscriptio tendinis but not extending to the mid-ventral line. The medialis is a straplike muscle not greatly expanded at the insertion and with its margins reasonably straight. The insertion is usually posterior to the tip of the mandible.

*M. geniohyoideus lateralis* (pl. LXXII, fig. G; LXXIV, fig. E).

The origin of the lateralis is on the posterior margin of the mandible dorsal and lateral to the medialis, except in *rostrata* where it is entirely lateral. The insertion is on the lateral edge and the dorsal surface of the ceratohyal beginning at, or slightly posterior to, a point caudad to the tip of the mandible and extending anteriorly to approximately the middle of the ceratohyal.

*M. rectus cervicis superficialis.*

The origin of this muscle is on the anterolateral edge of the sternum. The insertion is with the profundus at the inscriptio tendinis. In *robusta, nigroflavescens, subpalmata* and in an undescribed species the lateral fibers extend completely to the lateral margin of the profundus at the first myocomma anterior to the sternum. In the other species seen, the superficialis does not reach to the lateral margin of the profundus.

*M. rectus cervicis profundus.*

The profundus is an anterior extension of the rectus abdominis except for a few medial fibers which arise from the sternum. The insertion is on the ventral surface of the subarcualis rectus 1 and medially along the posterior edge of the inscriptio tendinis to the mid-ventral line. The muscle is divided into three segments. The posterior portion is the longest but is less than half the length of the entire muscle. The medial fibers of the anterior segment extend deep to the abdominohyoideus and the second ceratobranchial and are inserted on the floor of the mouth in all species except *macrinii* in which the lateral fibers extend to the ceratohyals, (pl. LXXII, fig. G; pl. LXXIII, fig. D; pl. LXXIV, fig. E). A series of short pharyngeal fibers extends from the insertion of the deep slip to the posteromedial edge of the ceratohyals. The anterior fibers form continuous caudal loops between the ceratohyals, but are not extended anteriorly between the closely approximating medial lobes of the ceratohyals.

*M. rectus cervicis lateralis.*

The origin of the lateralis is on the most lateral border of the sternum immediately lateral to the superficialis. It extends diagonally across the profundus to the lateral surface of the abdominohyoideus where it is inserted in fascia at the level of the thyroid gland. This muscle was not present in single specimens of *subpalmata* and *engelhardti.*

*M. subarcualis rectus 1* (pl. LXXII, fig. G).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning medially a short distance from the anterior end of the ceratohyal and extending caudad and caudolaterad approximately to the level of the posterior tip of the mandible. The fibers do not arise along the medial border as observed in other genera, but are near the center and along the lateral edge. The insertion is along the anterior edge of the inscriptio tendinis, deep to the lateral half of the geniohyoideus medialis, on the distal ends of the ceratobranchials and along the tendinous sheath surrounding the epibranchial. The muscle is long and extends several millimeters caudad to the posterior border of the front leg in all species.

*M. suprapeduncularis* (pl. LXXII, fig. G; pl. LXXIII, fig. D; pl. LXXIV, fig. E).

The fibers of the suprapeduncularis arise from the dorsomedial surface of the ceratohyal, beginning immediately posterior (approximately .5 mm.) to the anterior end of the ceratohyal and extending caudad for 1 or 2 mm. depending on the size of the specimen. The fibers are continuous between the ceratohyals and become progressively shorter from anterior to posterior. The muscle is much wider than long and appears as a smaller V-shaped muscle anterior to the medial lobes of the ceratohyals. The suprapeduncularis is distinctly separated from the pharyngeal muscles and the deep slip of the rectus cervicis by an elongate narrow space extending caudad from the suprapeduncularis between the medial lobes of the ceratohyals.

*M. hyoglossus.*

The origin of the hyoglossus is on the anterior tip of the basibranchial between the elongate cornus. The fibers extend fanwise and are inserted in the anterior tissues of the tongue.

## VARIATIONS IN THE HYOBRANCHIAL APPARATUS

In all *Magnadigita* the cornua of the first basibranchial are greatly elongated, being at least 1 mm. long in all species and in the larger species nearly 2 mm. The cornua extend anterolaterad from the basibranchial and are curved to nearly an anterior position at the tips.

The proximal ends of the ceratohyals terminate in blunt or rounded points only a short distance beyond the origin of the suprapeduncularis muscle. The anterior medial margins are straight and are directed slightly mediad so that a deep V-shaped space, partially occupied by the suprapeduncularis, is formed. The concavity present along the medial margins in other genera is indicated only in *robusta.* Furthermore the space separating the ceratohyals posterior to the suprapeduncularis muscle is extremely narrow in all species except *dunni.* The ceratohyals are widest near the posterior edge of suprapeduncularis and are narrow and attenuated distally. Posterior to the angle of the jaws, the ceratohyals curve at less than a ninety-degree angle, and their most distal tip is attached to the squamosal by a ligamentous sheath.

## SUMMARY

An attempt to establish, on the basis of the throat masculature and the hyobranchial cartilages, an intrageneric relationship of the species of this genus would be most difficult. The muscles and muscle patterns as well as the size and shape of the ceratohyals are rather uniform. However, I have come to regard *robusta* as the most primitive of the species, mainly because of the primitive origin of the quadrato-pectoralis and the presence of a large mass of pharyngeal fibers between the anterior ends of the deep slip of the rectus cervicis and the suprapeduncularis muscles. The fact that it is a terrestrial species also suggests a primitive status. The species *subpalmata* is also a generalized one, but is more specialized than *robusta.* The muscle patterns of *engelhardti, nigroflavescens, dunni,* and *franklini* are similar and represent the most specialized forms of the genus. Together these four form a series of closely related species, of which *engelhardti,* with its narrow specialized intermandibularis anterior and with the origin of the quadrato-pectoralis entirely free of the quadrate, is the most specialized.

The intermandibularis anterior is extremely variable in this genus; it is probably in the process of becoming reduced and may eventually be lost to the species of this genus.

## The GENUS *Bolitoglossa* Duméril and Bibron

*Bolitoglossa* Duméril and Bibron, 1854, Erpétologie général de l'histoire naturelle complete des Reptiles. vol. IX, p. 88. (type *mexicana*).

The genus *Bolitoglossa* includes the largest series of species of any of the Mexican and Central American genera. In all there are at least twenty-five species, three of which are as yet undescribed. The species are adapted mainly for arboreal life but some are known to live on the ground and under rocks.

The greater number of known species inhabit Mexico and Central America but some are also known from South America, giving the genus a very extensive range.

The species belonging to the genus *Bolitoglossa* are readily distinguished from all other plethodontids by the presence of a heavy glandular webbing on the hands and feet, from which only the tips of the middle digits may be free, giving to both hands and feet a palmate appearance. They are also characterized by the complete absence of the sublingual fold.

The following description of the hyobranchial apparatus and its musculature will set forth the myological characteristics of the genus.

### THE TRANSVERSE THROAT MUSCLES

*M. intermandibularis anterior* (pl. LXX, figs. G, H, I & J).

The origin of this muscle is variable; in *rufescens* and *striatula* the fibers arise from fascia immediately medial to the mandible, while in other species studied the fibers arise from fascia along the anterior edge of the anterior slip of the intermandibularis posterior. In *rufescens* and *striatula* the fibers are nearly parallel to those of the anterior slip of the intermandibularis posterior, but are easily distinguished by the absence of the median raphe. In an undescribed species from Costa Rica, the muscle is completely divided at the mid-ventral line. The muscle is small in all species and may vary considerably among the individuals of a species. In three specimens of *flaviventris*, the size (width) ranged from an extremely small narrow muscle to one as large as any observed in other species of the genus. This muscle may be absent in some species.

*M. intermandibularis posterior* (pl. LXX, figs. G, H, I & J).

The *anterior slip* originates on the dorsomedial surface of the mandible approximately one third of the length of the mandible from the symphysis. The insertion is in the ventral aponeurosis lateral to the mid-ventral line in all species examined. In *rufescens* and *striatula*, the anterior fibers extend only slightly more than half way to the mid-ventral line, whereas in *occidentalis* the fibers extend nearly to the mid-line. The line of insertion may be convex as in *rufescens*, straight as in *striatula*, concave as in *occidentalis*, or irregular as in *flaviventris*. In one specimen of the last species there is a middle slip extending mediad from its origin on the dorsal surface of the mandible between the two normal slips. It is inserted in the ventral fascia. The anterior part is deep to the anterior slip and the posterior part superficial to the posterior slip. This is another example of the variation obtaining in *flaviventris*.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible. The insertion is in the ventral aponeurosis. The muscle is fan-shaped and extends as far medially as the fibers of the anterior slip. The posterior fibers are nearly transverse and are inserted anterior to a line between the posterior tips of the mandibles.

*M. gularis* (pl. LXX, figs. G, H, I & J).

The origin of the gularis is entirely in fascia, the anterior portion arising from a thin aponeurosis which is attached to the lateral edge of the mandible and extends dorsad along the quadrate, squamosal and the lateral margin of the otic capsule. The posterior portion arises from the fascia cephalodorsalis and from the skin superior and dorsomedial to the fascia. The greater part of the insertion is on the skin of the gular fold, but approximately one third of the insertion is on the linea alba. No fibers reach the mid-ventral line; however, in most species the opposing gularis muscles are separated only by a distance of about one millimeter. The posterior tip of the mandible is always covered by the gularis.

*M. depressor mandibulae anterior* (pl. LXXII, fig. I).

The anterior muscle originates on the squamosal and the caudolateral edge of the otic capsule immediately dorsal to the squamosal. The part arising from the otic capsule is usually deep to the cucularis major. The insertion is on the dorsal half of the posterior tip of the mandible.

*M. depressor mandibulae posterior* (pl. LXXII, fig. I).

The posterior muscle originates in the fascia cephalodorsalis deep to the gularis. The insertion is on the ventral half of the posterior tip of the mandible.

*M. quadrato-pectoralis* (pl. LXX, figs. G, H, I & J).

This muscle arises in the angle formed by the attachment of the ceratohyal to the skull, being attached to the posterior edges of the quadrate and squamosal, and the ventral margins of the ceratohyal near its attachment to the skull. These surfaces are used in varying degrees by all species for the attachment of this muscle. In *platydactyla, flaviventris* and *mexicana* the dorsal tip of the quadrate gives rise to the majority of the fibers while in *rufescens* most of this muscle originates on the squamosal and there are no fibers attached to the quadrate. The tendinous mass around the ceratohyal gives rise to a small part of this muscle in all species. The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis. A few of the anterior and posterior fibers are deep to the adjoining muscles.

The origin, insertion and shape of this muscle is reminiscent of the relations existing in the genus *Magnadigita*.

*M. interhyoideus* (pl. LXX, figs. G, H, I & J).

The origin of the interhyoideus is on the anteroventral surface of the ceratohyal between the attachment of the ceratohyal to the skull and the angle of the ceratohyal posterior to the caudal tip of the mandible. The insertion is in the ventral aponeurosis deep to the intermandibularis posterior but with a few of the posterior fibers deep to the quadrato-pectoralis. The usual decussation of the fibers is present in all species.

### THE LONGITUDINAL AND DEEP MUSCLES

*M. geniohyoideus medialis* (pl. LXXI, fig. B; pl. LXXII, fig. A). The origin of the medialis is on the posterior edge of the mandible immediately lateral to the symphysis. In *striatula* the origin extends less than half the distance from the symphysis to the origin of the anterior slip of the intermandibularis posterior, whereas in *platydactyla* the origin extends for approximately three fourths of the distance. The insertion is lateral on the ventral surface of the subarcualis rectus 1 and medial along the inscriptio tendinis. The insertion does not extend to the mid-ventral line; it is however, very near the mid-line in *flaviventris* but fails to reach it by at least half its width in the other species. The lateral fibers are inserted at the level of the posterior tip of the mandible or posterior to it in all species.

*M. geniohyoideus lateralis* (pl. LXXI, fig. B; pl. LXXII, fig. A). The origin of the lateralis is on the posterior edge of the mandible dorsal and lateral to the medialis. In *striatula* the entire muscle is lateral, while in *platydactyla* all except the most lateral fibers are dorsal to the medialis. These two species represent the extremes, the other species varying between them. It is only in *striatula* that the lateralis originates entirely dorsal to the medialis. The insertion is on the lateral and dorsal surface of the ceratohyal, beginning at the level of, or slightly caudad to, the posterior tip of the mandible and extending anteriorly approximately to the middle of the cartilage.

*M. rectus cervicis superficialis* (pl. LXXI, fig. B; pl. LXXII, fig. A). The origin of this muscle is on the anterolateral edge of the sternum extending from the linea alba caudolaterad to the lateral tip of the sternum. The insertion is with the profundus and will be noted in the description of that muscle. In *Bolitoglossa* the superficialis is a rather narrow muscle and is medial to the lateral edge of the profundus in all species examined.

*M. rectus cervicis profundus* (pl. LXXI, fig. B; pl. LXXII, fig. A). The greater part of this muscle is a continuation of the rectus abdominus, with only a small medial part arising from the lateral edge of the sternum. The insertion is on the ventral surface of the subarcualis rectus 1 and anteromedial along the posterior edge of the inscriptio tendinis to the mid-ventral line. This muscle is divided by two myocommata into three unequal segments. In *rufescens, striatula* and *mexicana* the posterior segment is shorter than the combined lengths of the two anterior segments, in *flaviventris* it is approximately equal to the two anterior segments, and in *platydactyla, occidentalis* and two undescribed species it is longer. The medial fibers of the anterior segment extend deep to insert on the floor of the mouth a short distance posterior to the ceratohyals. Between the insertion and the ceratohyals is a short muscle appearing much the same as in *Magnadigita subpalmata.* The only exception is *rufescens* in which the intervening muscle fibers are absent and the deep slip is extended slightly more anteriorly than in other species.

*M. rectus cervicis lateralis.*

In spite of careful disections and observations of many species the lateralis muscle was seen only in *mexicana.* In large examples of both *platydactyla* and *flaviventris* not the slightest indication of it could be found. The origin in *mexicana* is on the extreme lateral edge of the sternum, noticeably lateral to the superficialis muscle. From the origin the fibers extend diagonally across the profundus and are inserted in fascia on the lateral surface of the abdominohyoideus near the level of the thyroid gland.

The lateralis muscle in *mexicana* is not particularly different from the lateralis of *Magnadigita* or *Pseudoeurycea.* The most important consideration lies in the fact it is absent from such a large segment of the genus *Bolitoglossa.*

*M. subarcualis rectus 1* (pl. LXXI, fig. B; pl. LXXII, figs. A & I).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning a short distance from the anterior end of the ceratohyal and extending posteriorly along the lateral and medial margins. The fibers along the lateral side of the ceratohyal extend farther posteriorly than do those on the medial edge, however in *Bolitoglossa* the difference is not nearly as great as in other genera. In *mexicana* the lateral row of fibers is interrupted by a short diastema in which no fibers are attached to the ceratohyal. In *rufescens* only a small posterior portion of the lateral row of fibers has been retained.

*M. suprapeduncularis* (pl. LXXIII, figs. A & F).

The origin of the suprapeduncularis is on the dorsomedial surface of the ceratohyals immediately caudal to their anterior tips. In size and shape this muscle is much the same as it is in *Magnadigita.* In *platydactyla* the posterior fibers are almost as long as the anterior fibers and the muscle is divided into four rather distinct bundles. In an undescribed species from Mexico this muscle is very small and has been pushed anteriorly by the wide contact of the ceratohyals posterior to the muscle.

*M. hyoglossus.*

The origin is on the anterior margin of the tip of the basibranchial. The surface is between the cornua and does not extend to any part of the ventral surface. The origin and insertion of the hyoglossus and the length and shape of the cornua are very similar, even in details, to the conditions obtaining in the genus *Magnadigita.*

### VARIATIONS IN THE HYOBRANCHIAL APPARATUS

The ceratohyals in *Bolitoglossa* are essentially the same as described for *Magnadigita.* In *rufescens* the shape and general appearance is similar, except that the entire hyobranchial structure is noticeably posterior to that of other species of *Bolitoglossa.*

## SUMMARY

In *Bolitoglossa* the entire throat musculature and the hyobranchial skeleton are similar to the conditions found in *Magnadigita.* The main difference between the two genera lies in the absence of the rectus cervicis lateralis from the large majority of species of *Bolitoglossa.* The myology in both is generalized and compares rather well with many of the muscle patterns in the generalized species of the genus *Pseudoeurycea.*

The species *platydactyla* appears to be the most primitive of the genus *Bolitoglossa* at least among the species studied. The origin of the quadrato-pectoralis, the elongate posterior fibers of the suprapeduncularis, the unspecialized geniohyoideus muscles, and the large mass of pharyngeal muscles between the deep slip of the rectus cervicis and the suprapeduncularis mark it as primitive. The presence of the rectus cervicis lateralis in *mexicana* marks it as a primitive species, although I consider it to be more specialized than *platydactyla,* because of the reduced pharyngeal muscles and the smaller extent of the insertions.

The small *rufescens* is obviously the most specialized as well as the most aberrant species of the genus. The primary specializations of *rufescens* are to be found in the origin of the subarcualis rectus 1, in the origin of the quadrato-pectoralis on the squamosal and not on the quadrate, and in the noticeably posterior position of the ceratohyal. From the nature of the throat anatomy, *rufescens* appears to be closely related to *striatula* and *occidentalis.* It may also be allied to *lignicolor* and *colonnea,* both of which are unknown to me.

There are obviously two major groups of species in the genus. The first includes the larger species, *platydactyla, flaviventris* and *mexicana;* and the second includes the smaller species *occidentalis,* two undescribed species, and possibly *rufescens.* The last species, although not entirely typical, does have many affinities to the species of the second group and is best placed with them rather than as a separate group. A rather noticeable difference between *rufescens* and other bolitoglossids is the more pointed nature of the jaws at the symphysis. In all other forms the jaws are much more rounded, even in species such as *occidentalis,* which appear to be most closely related to it.

The myology of *striatula* is not typical of either group. As regards the origin of the quadrato-pectoralis, it is like that of the first group, but in many other characters already noted, *striatula* is similar to *rufescens* or is unique as in the origin of the geniohyoideus lateralis.

## GENUS *Oedipina* Keferstein

*Oedipina* Keferstein, Nachr. Ges. Göttingen, vol. 15, 1868, p. 331 (type *uniformis*).

The genus *Oedipina* includes at least ten species of greatly elongate, wormlike, terrestrial salamanders. They are characterized, by having small legs, a tail which is usually much longer than the combined length of the head and body; fully webbed digits with only the tips free and more or less pointed or rounded and by having seventeen to twenty costal grooves. The adpressed limbs are separated by half or more of the costal grooves present.

The following myological considerations are based almost entirely on *uniformis, complex, parvipes* and on two undescribed species. The types of *serpens* and *syndactyla* were seen, but were not dissected except to determine the origin of the M. geniohyoideus lateralis and the shape of the anterior part of the ceratohyals.

### THE THROAT MYOLOGY AND THE HYOBRANCHIAL APPARATUS

### TRANSVERSE THROAT MUSCLES

*M. intermandibularis anterior* (pl. LXX, fig. D).

The origin of this muscle is in a small flattened straplike fascia extending from the muscle laterad to attach to the dorsomedial surface of the mandible. Both the anterior and posterior edges of the muscle are slightly convex with the greatest width occurring medially. There is no indication of a median raphe. This muscle is very uniform in the species examined.

*M. intermandibularis posterior* (pl. LXX, fig. D).

The *anterior slip* arises on the dorsomedial surface of the mandible and extends fanwise medioventrad between the lateral and medial part of the geniohyoideus lateralis to insert in the ventral aponeurosis. The fibers of the entire muscle are directed caudomediad with the most anterior ones nearly transverse and inserted at the median raphe.

The *posterior slip* arises on the dorsomedial surface of the mandible, beginning less than one millimeter from the posterior tip of the mandible and extending anteriorly for slightly more than one third the length of the mandible. From the origin it extends as a broad fan-shaped muscle and is inserted in the ventral aponeurosis.

*M. gularis* (pl. LXX, fig. D).

The origin of the gularis is entirely in fascia. The anterior portion (approximately half) arises in a thin aponeurosis which is attached to the quadrate, the squamosal, and the fascia covering the muscles of the otic region. The posterior portion arises from the fascia cephalodorsalis and the skin immediately above it. This muscle is almost completely inserted on the skin of the gular fold, except that a few of the most anterior fibers are inserted in the median raphe. In *complex* and *parvipes* the anterior fibers are just short of the median raphe. In these two species this muscle is also slightly caudad to the tip of the mandible, exposing the insertion of the depressor mandibulae.

*M. depressor mandibulae anterior.*

The anterior muscle arises from the posterolateral edge of the quadrate, from the squamosal and from the lateral border of the otic capsule. The insertion is on the dorsal half of the posterior tip of the mandible. In all species except *complex,* the fibers arising from the otic capsule lie deep to the cucularis major.

*M. depressor mandibulae posterior.*

The posterior muscle originates in the fascia cephalodorsalis deep to the gularis but superior to the cucularis major. The insertion is on the ventral surface of the posterior tip of the mandible.

*M. quadrato-pectoralis* (pl. LXX, fig. D).

The origin of this muscle is mainly on the posterior border and the ventral surface of the squamosal, but the more anterior fibers extend beneath the squamosal and arise from the lateral edge of the otic capsule deep to the dorsal part of the squamosal. This condition is singular in the genus *Oedipina.* The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis. The anterior and posterior fibers may or may not insert deep to the intermandibularis and gularis. In *parvipes* the most posterior fibers insert on the medial part of the gular fold.

*M. interhyoideus.*

The origin of the interhyoideus is on the anteroventral surface of the ceratohyal, beginning near the distal edge of its dorsal curve and extending for approximately two thirds of the distance to its attachment on the squamosal. It is widely separated from the origin of the quadrato-pectoralis. The insertion of this muscle is in the ventral aponeurosis. However, in *parvipes, complex,* and an undescribed species (number 1419) it is entirely deep to the intermandibularis posterior. In *uniformis* and in a second undescribed species (number 2504) the insertion is deep to the anterior part of the quadrato-pectoralis and to the posterior part of the intermandibularis posterior.

### THE LONGITUDINAL AND DEEP MUSCLES

*M. geniohyoideus medialis* (pl. LXXII, fig. D).

The origin of the muscle is on the posterior surface of the mandible at and immediately lateral to the symphysis. The origin is very narrow, approximately one third the width of the insertion, except in specimen No. 1419 where the lateral fibers lie deep to the median part of the lateralis and provide for a slightly greater width at the origin. In *uniformis* a few of the deep fibers arise from the floor of the mouth a short distance caudad to the fibers originating on the mandible. The insertion is on the ventral surface of the subarcualis rectus 1 and medially along the anterior edge of the inscriptio tendinis. The insertion does not reach the mid-ventral line. The muscle is not straight but curved laterad. The curving is particularly evident along the lateral margin of the muscle, and the insertion is caudad to the posterior tip of the mandible in all species.

*M. geniohyoideus lateralis* (pl. LXXII, fig. D).

The origin of the lateralis is on the ventral and posterior surface of the mandible lateral to the medialis. The origin is wide, extending laterad from the medialis until it is divided by the intermandibularis anterior and the anterior slip of the intermandibularis posterior. From this point it continues caudad at least to a point level with the center of the eye. In specimen No. 1419 the origin extends to the posterior edge of the eye and is attached along approximately half of the mandible. The insertion is on the lateral and dorsal surfaces of the ceratohyal, beginning caudad to the posterior tip of the mandible and extending anteriorly approximately to the middle of the cartilage. Those fibers arising mediad to the division extend deep to the lateral fibers and are inserted dorsal to the lateral fibers.

*M. rectus cervicis superficialis* (pl. LXXII, fig. D).

This muscle arises on the anterolateral margin of the sternal cartilage, and extends anteriorly to the first myocomma where it becomes fused with the profundus. The superficialis does not reach the lateral edge of the profundus at the first myocomma.

*M. rectus cervicis profundus* (pl. LXXII, fig. D; pl. LXXIV, fig. D).

The major portion of this muscle is a direct continuation of the rectus abdominis but a few of the most medial fibers do arise from the lateral edge of the sternum. The insertion is with the superficialis on the ventromedial surface of the subarcualis rectus 1, and medially along the posterior edge of the inscriptio tendinis to the mid-ventral line. The insertion of the more median fibers is directly ventrad to the first ceratobranchial. This muscle is divided into three segments of nearly equal length. The anterior and posterior segments are nearly equal in length while the middle one is usually slightly shorter than either of the other two. In *parvipes* the posterior segment is noticeably longer. From the medial part of the anterior myocomma deep to the superficial portion of the muscle, a small slip extends anteriorly to insert on the floor of the mouth. The medial fibers of the deep slip are longer than the lateral fibers but do not extend entirely to the suprapeduncularis.

*M. subarcualis rectus 1* (pl. LXXII, fig. D; pl. LXXIV, fig. D).

The origin of this muscle is on the ventral, ventrolateral and posterior surfaces of the ceratohyal, beginning in the median part of the ceratohyal at approximately the level of the anterior edge of the suprapeduncularis and extending caudad to the posterior edge of the cartilage, along its posterior margin for a short distance and then across its ventral surface to the lateral border. The lateral part of the muscle extends posterior to the level of the caudal tip of the mandible. The insertion is along the anterior edge of the inscriptio tendinis from the mid-ventral line laterad to the distal ends of the cerato-branchials and caudally along the tendinous sheath surrounding the elongate epibranchial. The fibers of the medial half of the muscle are much shorter in typical *Oedipina* than obtains in other genera studied. The muscle extends beyond the anterior edge of the front leg in all species seen. It is shortest in *complex* and *parvipes* and longest in *syndactyla* and specimen No. 1419.

A small elongate slip quite apart from the main mass of the muscle arises in a tendinous fascia, which is attached to the ventral surface of the ceratohyal anterior to the suprapeduncularis. The insertion is on the ventral surface of the subarcualis rectus 1 deep to the lateral half of the geniohyoideus medials. The insertion of this muscle is fused with the insertion of the subarcualis rectus 1 and appears to be a specialized slip of this muscle. However, it should be pointed out that except for the insertion the slip is completely separate and distinct from the main muscle, and may represent a new muscle, peculiar to the genus *Oedipina.*

*M. suprapeduncularis* (pl. LXXIV, fig. D).

The origin of the muscle is on the dorsomedial surface of the ceratohyal, beginning at the base of the attenuated proximal end of the ceratohyal and extending caudad beyond the narrowest space between the two ceratohyals. The muscle is broad for its entire width and the most posterior fibers are the longest. Both conditions are peculiar to the genus *Oedipina.*

*M. hyoglossus.*

The origin of the hyoglossus is on the anterior tip of the basibranchial between the diagonal cornua. There are no fibers arising from the ventral surface of the anterior tip of the basibranchial as observed in the genus *Chiropterotriton.* The insertion is in a semicircle along the anteroventral surface of the tongue. The fibers are in 6-8 small bundles, rather than in a thin sheet.

### VARIATIONS IN THE HYOBRANCHIAL APPARATUS

The anterior ends of the ceratohyals are long and attenuated but are not round and rodlike as in *Thorius.* Medially they are flattened, but lack the medial lobe, which in other genera constricts the posterior part of the suprapeduncularis. Distally they are also attenuated and are curved at more than a ninety degree angle posterior to the tip of the mandible. The ceratohyals are attached to the squamosal by a ligamentous sheath.

## Summary

The genus *Oedipina* consists of an uniform assemblage of specialized species. The specializations have not been restricted to one or two muscles but are evident in most of them, particularly in the longitudinal and deep muscles. The ceratohyals have been noticeably modified. These specializations are, however, rather uniform among the species within the genus and it is quite impossible to refer to any one species as being more generalized than other members of the genus. In no other genus have I encountered such a uniform series of muscular patterns.

### GENUS *Lineatriton* Tanner

*Lineatriton* Tanner, 1950, Great Basin Nat., vol. X, pp. 37-44.

The genus *Lineatriton* as it is now constituted includes only the Mexican terrestrial wormlike salamander *Lineatriton lineola.* This species was formerly included in the genus *Oedipina,* presumably because of its similarity to the species of *Oedipina* in outward appearance and in habitat preference rather than in other characters. Anatomically *L. lineola* has many myological and skeletal (vertebral and hyobranchial) characters that are decidedly different from those found in *Oedipina.*

In spite of the fact that *L. lineola* has reduced the size of its legs, developed a tail as much as twice the length of the head and body, and has taken on a snakelike appearance, it can still be readily distinguished externally from any of the other wormlike salamanders by the reduced number of costal grooves (14) and by the partially free middle digits.

In the following descriptions of the throat musculature and the hyobranchial apparatus other significant anatomical differences between the species *L. lineola* and the species of the genus *Oedipina* will be indicated.

#### TRANSVERSE THROAT MUSCLES

*M. intermandibularis anterior* (pl. LXIX, fig. E).

The origin of this muscle is in a small straplike fascia approximately .2 mm medial to the mandible and deep to the anterior edge of the anterior slip of the intermandibularis posterior. The fascia is attached to the mandible and there is no median raphe at the mid-ventral line. Both the anterior and posterior margins are convex and the greatest width, .4 mm., occurs at the mid-ventral line.

*M. intermandibularis posterior* (pl. LXIX, fig. E).

The *anterior slip* originates on the dorsomedial surface of the mandible approximately 1.3 mm. from the symphysis. The fibers extend fanwise from the origin in a more or less caudomedial direction. Approximately the anterior fifth of the muscle inserts at the median raphe and there is a broad contact posteriorly with the anterior fibers of the posterior slip.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible. The insertion is in the ventral aponeurosis and extends anteriorly from a line between the posterior tips of the mandibles, to occupy half or more of the distance to the symphysis. The median and posterior fibers extend nearly to the mid-ventral line.

*M. gularis* (pl. LXIX, fig. E).

The origin of the gularis is in fascia. The anterior part arises in an aponeurosis which is attached to the mandible, quadrate, squamosal and on the muscles and fascia of the otic capsule. The posterior part arises in the fascia cephalodorsalis and from the skin superior to it. The insertion is on the skin of the gular fold and in the ventral fascia along the linea alba. Approximately one third of the insertion is in the ventral fascia (.8 mm.). This is twice the length of the insertion observed in five species of *Oedipina.*

*M. depressor mandibulae.*

The *anterior muscle* arises on the squamosal and otic capsule, the latter part being deep to the cucularis major. The insertion is on the dorsal half of the posterior tip of the mandible.

The *posterior muscle* originates in the fascia cephalodorsalis deep to the gularis but superior to the cucularis. The insertion is on the ventral half of the posterior tip of the mandible.

Both muscles are distinctly separated from origin to insertion.

*M. quadrato-pectoralis* (pl. LXIX, fig. E).

The origin of the muscle is mainly on the posterior edge of the squamosal, but a few medial fibers arise from the dorsal tip of the quadrate. There are no fibers extending deep to the squamosal to arise from the ventral surface of the squamosal and the otic capsule as in the genus *Oedipina.* The insertion is in the ventral fascia between the gularis and the intermandibularis posterior. The anterior fibers are inserted deep to the intermandibularis and the posterior fibers reach the linea alba.

*M. interhyoideus.*

The origin of the interhyoideus is on the anteroventral surface of the ceratohyal beginning at the curve directly caudad to the posterior tip of the mandible and extending craniad at least half way to the attachment of the ceratohyal to the skull. The insertion is in the ventral aponeurosis deep to the posterior part of the intermandibularis posterior. A few fibers insert with the most anterior fibers of the quadrato-pectoralis. The muscle appears to be larger in *L. lineola* than in *Oedipina* of comparable size.

### THE LONGITUDINAL AND DEEP MUSCLES

*M. geniohyoideus medialis* (pl. LXXII, fig. B).

The origin of the medialis is on the posterior surface of the mandible, beginning at the symphysis and extending laterad for approximately .7 mm. There are no fibers arising from the ventral surface of the mandible and the width of the muscle at the origin is nearly twice as wide as in any species of the genus *Oedipina.* The insertion is on the ventral surface of the subarcualis rectus 1, and mediad along the inscriptio tendinis. The muscle at the insertion is only slightly wider than the origin and the medial edge of the insertion is at least half the width of the muscle from the midventral line. The entire insertion is posterior to the caudal tips of the mandibles.

The geniohyoideus medialis is a broad straplike muscle with nearly straight margins for its entire length, not curved or of a variable width as is characteristic of the genus *Oedipina.*

*M. geniohyoideus lateralis* (pl. LXXII, figs. B & H).

The origin of the lateralis is on the posterior surface of the mandible, mostly lateral to, but with a few medial fibers dorsal to, the medialis. The entire origin lies anterior to the origin of the anterior slip of the intermandibularis posterior and the muscle is completely dorsal to both slips of the intermandibularis. The insertion is on the lateral edge and the dorsal surface of the ceratohyal, beginning at a point just caudad to the posterior tip of the mandible and extending anteriorly to a point near the middle of the ceratohyal.

The geniohyoideus lateralis of *lineola* is simple in structure and has not undergone the specializations existing in *Oedipina.* Actually the origin, insertion, size, shape and general character of this muscle is strikingly similar to that obtaining in the genus *Pseudoeurycea* and is nowise reminiscent of the conditions found in the typical species of *Oedipina.*

*M. rectus cervicis superficialis* (pl. LXXII, figs. B & H).

The origin of this muscle is on the anterolateral edge of the sternum. From the origin the fibers extend anteriorly along the mid-line and anterolaterad to reach the lateral edge of the profundus at the first myosepta. From this point anteriorly the superficialis and profundus are fused. The insertion is with the profundus. In *Oedipina* the superficialis is proportionately narrower and does not extend to the lateral edge of the profundus.

*M. rectus cervicis profundus* (pl. LXXII, fig. B).

The lateral and larger part of the profundus muscle is a direct continuation of the rectus abdominis; while a much smaller medial part arises from the lateral edge of the sternum deep to the superficialis. The muscle inserts laterally on the ventral surface of the subarcualis rectus 1 and medially along the inscriptio tendinis to the mid-ventral line. From the medial part of the anterior myosepta a small slip extends deep to the abdominohyoideus and the second ceratobranchial to insert on the floor of the mouth posterior to the suprapeduncularis and the ceratohyals.

In *lineola* the rectus cervicis is divided into three unequal segments. The middle segment is the shortest and the posterior one is more than twice the combined lengths of the other two. This is quite different from the conditions found in *Oedipina* and is again very similar to the rectus cervicis of *Pseudoeurycea.*

*M. rectus cervicis lateralis* (as in pl. LXXI, fig. C).

The origin of the lateralis is on the lateral edge of the sternum immediately laterad to the superficialis. The insertion is in fascia on the lateral side of the abdominohyoideus, near the level of the posterior end of the thyroid gland.

*M. subarcualis rectus 1* (pl. LXXII, figs. B & H).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning approximately at the level of the anterior edge of the suprapeduncularis where the muscle curves mediad and laterad to the margins of the ceratohyal. The medial part extends caudad along the inner edge for a short distance only, whereas the lateral part extends beyond the posterior tip of the mandible. The insertion extends from the mid-ventral line, laterad along the inscriptio tendinis to the distal ends of the ceratobranchials, and caudally along the tendinous sheath surrounding the epibranchials.

The muscle extends for at least .2 mm. beyond the posterior border of the front leg and is a proportionally longer muscle in *lineola* than in any of the species of the genus *Oedipina.*

*M. suprapeduncularis* (pl. LXXII, fig. H).

In *lineola* the suprapeduncularis is a small muscle, approximately as wide as it is long and with the fibers noticeably shortened near the posterior border. It lies between the dorsomedial surface of the ceratohyals and extends as a thin transverse muscle across the stalk of the tongue. The origin begins at the base of the anterior spade of the ceratohyal and extends posterior until the ceratohyals approximate each other, by means of the median lobes, at the mid-ventral line. At no point are the fibers more than .5 mm. long.

*M. hyoglossus.*

The origin is on the anterior edge of the basibranchial between the base of the cornua. The fibers extend fanwise into the tissue of the tongue anterior to the origin.

### VARIATIONS IN THE HYOBRANCHIAL APPARATUS

The proximal ends of each ceratohyal extend anterior as a flattened, lobate, spadelike structure, with the thin medial edges almost in contact at the mid-ventral line. The small suprapeduncularis fits into a concavity between the anterior and the median lobes. The distal ends of the ceratohyals are attenuated, curved at less than a ninety degree angle, and attached to the squamosal by a ligament, as they are in the other genera.

The relative size and shape of the ceratohyals and of the suprapeduncularis muscle in *lineola* is so similar to the same structure in *Pseudoeurycea*, and is completely different from that obtaining in *Oedipina.*

### SUMMARY

The species *Lineatriton lineola* is primitive and manifests the more generalized muscle patterns which were presumably present in the ancestral stock of the majority of Mexican salamanders. It is anatomically not closely related to the species of *Oedipina.* This is clearly shown by the entirely different origin of the M. quadratopectoralis, geniohyoideus medialis and geniohyoideus lateralis, and by the distinct variations in the size and shape of the rectus cervicis, the suprapeduncularis and by the equally important diversity in the size and shape of the ceratohyals. The entire anatomical arrangement of the hyobranchial apparatus and its musculature is reminiscent of the general relationship of parts existing in *Pseudoeurycea, Chiropterotriton* and *Parvimolge.* The relationship of *Lineatriton* to *Oedipina* is then, entirely superficial and may best be considered as an excellent example of parallelism in development.

## GENUS *Thorius* COPE

*Thorius* Cope, 1869, Proc. Acad. Nat. Sc. Philadelphia, p. 111. (type *pennatulus*).

The genus *Thorius,* as now restricted, includes seven species of diminutive terrestrial salamanders. Together they form a uniform group decidedly distinct from other Mexican and Central American genera. They are recognized by the presence of an orbitolabial groove, a sublingual fold, a poorly ossified skull, particularly in the dorsal parietal region and by enlarged nostrils. The complete absence of maxillary teeth is also an important characteristic.

The throat muscles are remarkably uniform and show only slight variations in the relative size and shape among the several species. When the throat musculature of *Thorius* is compared with that of other genera the absence of the intermandibularis anterior and the presence of other specializations to be discussed presently, indicates that the genus is as distinct in its myology as it is in external and osteological characters.

### THE THROAT MYOLOGY AND THE HYOBRANCHIAL APPARATUS

### TRANSVERSE THROAT MUSCLES

*M. intermandibularis anterior.*

Careful dissection and tissue staining has failed to show any trace of this muscle. I have therefore concluded that it is absent in all species of the genus *Thorius.*

*M. intermandibularis posterior* (pl. LXVIII, fig. E; pl. LXX, fig. F).

The *anterior slip* originates on the dorsomedial surface of the mandible; the origin is located caudomediad from the symphysis approximately one third to two fifths the length of the mandible. The fibers extend fanwise from the narrow origin and are inserted in the ventral aponeurosis. In *Thorius* there are no fibers inserted along the mid-ventral line. Except for the anterior fibers, which are for the most part transverse, the fiber direction is caudomediad.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible and is inserted in the ventral aponeurosis. This slip is large, fan-shaped, with the anterior fibers extending anteromedially and the posterior fibers extending, slightly caudomedially from the origin to the insertion. No fibers reach the mid-ventral line.

The anterior slip of the intermandibularis posterior in *Thorius* is not enlarged to compensate for the loss of the intermandibularis anterior as it is in the case of *Chiropterotriton abscondens.*

*M. gularis* (pl. LXX, fig. F).

The origin of the gularis is in fascia, which is attached to the quadrate and squamosal elements, it attaches caudally along the postocular skin-groove and the fascia cephalodorsalis, extending back to, or almost to, the gular fold, except in *minutissimus,* in which it arises entirely from the postocular groove. The anterior half arises in an aponeurosis while the posterior half originates in fascia extending along the skin and the muscles underlying the postocular fold. The insertion is on the skin of the gular fold. The anterior fibers do not reach the mid-ventral line.

In all species this muscle is caudad to the posterior tip of the mandible, thus clearly exposing the insertion of the *M. depressor mandibulae.* In *minutissimus* the depressor mandibulae anterior is entirely exposed.

*M. depressor mandibulae anterior* (pl. LXX, fig. F).

The anterior muscle arises from the posterolateral edge of the quadrate, the dorsal surface of squamosal and the lateral edge of the otic region of the skull. The dorsal (otic) portion is deep to the cucularis major. The insertion is on the dorsal part of the posterior tip of the mandible.

*M. depressor mandibulae posterior* (pl. LXX, fig. F).

The posterior muscle arises from the fascia cephalordorsalis deep to the gularis and superior to the cucularis major. The insertion of the posterior muscle is on the ventral part of the posterior tip of the mandible.

*M. quadrato-pectoralis* (pl. LXX, fig. F).

The origin of the muscle is on the posterior edge of the squamosal with the major portion of it arising from a small posteriorly projecting osseous process. No fibers arise from the quadrate although some appear to arise from the ligament which attaches the ceratohyal to the squamosal. The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis.

*M. interhyoideus* (pl. LXX, fig. F).

The origin of this muscle is on the anteroventral edge of the distal end of the ceratohyal, approximately equidistant between the attachment of this cartilage to the skull, and the point where the ceratohyal is curved caudad to the angle of the jaw. The insertion is in the ventral aponeurosis deep to the posterior slip of the intermandibularis posterior. The interhyoideus is a small narrow muscle and is uniform in the genus *Thorius* except for a wider (.8 mm.) insertion in *troglodytes.*

### LONGITUDINAL AND DEEP THROAT MUSCLES

*M. geniohyoideus medialis* (pl. LXVIII, fig. E; pl. LXXII, fig. C).

The origin of the muscle is on the posterior margin of the mandible beginning at the symphysis and extending laterad for .2 to .5 mm. depending on the size of the specimen. The insertion begins on the ventrolateral surface of the subarcualis rectus 1 and extends medially across the ventral surface of the subarcualis rectus 1 to the lateral edge of the inscriptio tendinis. This muscle is uniform in width for its entire length and is slightly expanded only at its insertion. The insertion is not in a diagonal line but is nearly transverse and is noticeably lateral to the mid-ventral line. This muscle extends caudad to the posterior tip of the mandible in all species except *pennatulus,* in which it extends only to the level of the posterior tip of the mandible.

*M. geniohyoideus lateralis* (pl. LXVIII, fig. E; pl. LXXII, fig. C).

The origin of the muscle is on the posterior margin of the mandible lateral to the medialis muscle. There are no fibers arising from the mandible posterior to the anterior slip of the intermandibularis posterior. Some fibers do arise, however, from fascia immediately medial and caudal to the anterior slip. The insertion of this muscle is on the lateral edge and on the dorsal surface of the ceratohyal anterior to the lateral hook of the ceratohyal and extends anteriorly approximately to the middle of this cartilage. Some of the medial fibers extend caudad to the ceratohyal and insert on the floor of the mouth anterior to the deep slip of the rectus cervicis. The insertion extends caudad to the posterior tip of the mandible in all species except *pennatulus* where it is (approximately .2 mm.) anterior to the posterior tip. The belly and insertion are both much wider than the origin.

*M. rectus cervicis superficialis* (pl. LXXII, fig. C).

The origin of the superficialis is along the anterolateral edge of the sternal cartilage. The origin is narrow, less than half the distance from the mid-line to the lateral edge of the rectus cervicis profundus. The muscle extends anteriorly and anterolaterally to the lateral edge of the profundus at the first myocomma anterior to the sternum. An exception to this is found in *pulmonaris* in which the entire muscle is more narrow and does not reach to the lateral edge of the profundus. The insertion is with the profundus in the inscriptio tendinis.

*M. rectus cervicis profundus* (pl. LXVIII, fig. E; pl. LXXII, fig. C; pl. LXXIV, figs. A & B).

The major part of this muscle is a direct continuation of the rectus abdominis, however, a few fibers arise on the sternum deep to the lateral edge of the superficialis. The insertion of the lateral part of the muscle is on the ventral surface of the subarcualis rectus 1, while the medial portion inserts along the posterior edge of the inscriptio tendinis. At the anterior myocomma approximately the medial third of the muscle extends deep to the ceratobranchials and the abdominohyoideus to insert on the floor of the mouth. In *pennatulus* the lateral fibers of the deep slip reach the posterior edge of the ceratohyal. There are two myocommata and three unequal segments in this muscle, with the posterior segment approximately one and a half times as long as either of the other segments.

*M. rectus cervicis lateralis.*

Careful dissection and staining has failed to reveal any traces of this muscle in the genus *Thorius.*

*M. subarcualis rectus 1* (pl. LXXII, fig. C; pl. LXXIV, figs. A & B).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning at the base of the long attenuated anterior end of the ceratohyal, approximately at the anterior edge of the suprapeduncularis, and extending posteriorly along the medial margin of the ceratohyal. The origin of the lateral portion is much longer extending nearly to the posterior tip of the mandible. The medial part of the insertion is along the anterior edge of the inscriptio tendinis; the lateral part is inserted on the posterior ends of the ceratobranchials and along the tendinous sheath surrounding the epibranchial.

In *Thorius* this muscle is short, not extending posterior to the anterior edge of the front leg, except in *macdougalli* where it extends nearly to the posterior border of the leg. The posterior end of this muscle is noticeably rounded and more blunt than it is in other genera. In no other Mexican and Central American genus does this muscle fail to reach caudad to the anterior border of the front leg when the leg is placed at right angles to the body. In some *Chiropterotriton* (*chondrostega, dimidiata* and *chiroptera*) and in *Oedipina complex* and *O. parvipes,* the tip of the muscle reaches approximately to the posterior border of the front leg or slightly beyond. In all other *Chiropterotriton, Oedipina* and other genera here considered, the muscle extends posterior to the leg.

*M. suprapeduncularis* (pl. LXVIII, fig. E; pl. LXXIV, figs. A & B).

The muscle arises from the dorsomedial edge of the ceratohyal and extends as a thin transverse sheet dorsal to the stalk of the tongue. The fibers of the anterior portion are longest and in the shape of a broad U as they extend caudodorsally across the stalk of the tongue. It is a distinct muscle, quite apart from any other pharyngeal muscle and except in the case of the *pennatulus* it is separated from the deep slip of the rectus cervicis by its width or more. In *pennatulus* it is separated only by approximately half its width.

*M. hyoglossus.*

The origin is on the anterior tip of the basibranchial between the cornua. The insertion is in the substance of the tongue anterodorsal to the origin.

### VARIATIONS IN THE HYOBRANCHIAL APPARATUS

In all species of *Thorius* the anterior portion of the ceratohyal is extended into a long attenuated rod of cartilage and is in this respect different from all other Mexican and Central American plethodontids.

Hilton (1946:6), in his figures of the hyobranchial skeleton of *Thorius pennatulus*, shows the ceratohyals terminating anteriorly in a broad rounded lobe and the cornua extending at right angles to the basibranchial. In the text of his paper, however, he refers to the hyobranchial apparatus as "slender." I have found the ceratohyals to be greatly attenuated anterior to the suprapeduncularis, and have seen no indication of the ceratohyals becoming expanded and lobate as figured by Hilton (*op. cit.*). I have observed the short cornua extending in an anterolaterad direction from the tips of the basibranchial in all species of the genus. The cornua are certainly not transverse as figured by Hilton.

The most variable part of the apparatus is the size and shape of the ceratohyal. Three types of variation are represented by *pennatulus, macdougalli*, and *narisovalis.* (pl. LXVIII, fig. E; pl. LXXIV, figs. A, B & G). The ceratohyal of other species, not figured, are very similar to that of *narisovalis.*

## SUMMARY

The genus *Thorius* is unique in that none of its species have retained the intermandibularis anterior or the rectus cervicis lateralis. The extent of myological specialization now present in the species of *Thorius* is indicated by the fact that the loss of these muscles in species of other genera is the exception rather than the rule. The muscle patterns found in the various species of *Thorius* are remarkably uniform and vary only in minor details. Judged by variations in the hyobranchial apparatus and the throat musculature, *pennatulus* is the most variable species of the genus, whereas, *narisovalis* and *minutissimus* are the two most closely related species. Another characteristic feature of the genus *Thorius* worthy of emphasis is the specialization of the anterior part of the ceratohyal into an elongate attenuated rod. Such a modification is not found in the other genera of Mexican and Central American Plethodontidae.

## DISCUSSION AND SUMMARY OF THE GENERIC DIFFERENCES AND SIMILARITIES

That there are significant differences existing in the throat anatomy of the Mexican and Central American genera of the family Plethodontidae is evident from the foregoing descriptions.

The genus *Pseudoeurycea* is, as previously stated, apparently the most generalized of the genera under consideration. Its primitiveness is manifested by the broad insertions of the transverse ventral throat muscles, the attachment of the quadrato-pectoralis to the quadrate in the most primitive species, the comparatively large rectus cervicis lateralis, the extremely elongate condition of the subarcualis rectus 1, the broad insertion of the geniohyoideus medialis and the spadelike anterior lobes of the ceratohyal. The origins and insertions of the muscles studied are extensive and there are fewer apparent specializations in the throat myology than in other genera.

The genus *Chiropterotriton* appears to have developed from stock closely related to *Pseudoeurycea.* The origin and insertion of the gularis is only slightly less extensive than in *Pseudoeurycea* and is similar in these genera. The genus *Chiropterotriton* is unique in having the fibers of the hyoglossus arise from the ventral surface of the anterior end of the basiobranchial rather than from the anterior tip. This character is uniform in the genus and does not vary even in the aberrant species *abscondens.* Other variable characters in the genus *Chiropterotriton* are the variation of the origin of the geniohyoideus lateralis, the large size and triangular shape of the intermandibularis anterior and the reduced length of the subarcualis rectus 1.

The anterior lobes of the ceratohyals are similar to those of *Pseudoeurycea* but with this difference; the lateral edge is rather thick and there is a thinning medially giving the appearance of a "blade" rather than that of a spatula or spade.

The genus *Parvimolge* is myologically primitive. Its myology relates it to the genus *Pseudoeurycea,* but is suggestive of a more primitive condition than that of *Chiropterotriton. Parvimolge* is similar to *Pseudoeurycea* in several characters; the origin and insertions of the muscles are equally extensive, the intermandibularis anterior is not triangular, the origin of the geniohyoideus muscles is similar and the subarcualis rectus 1 is approximately of the same relative length. The overlapping position of the anterior lobes of the ceratohyals is unique, but the shape of the lobes resembles more closely that of *Pseudoeurycea* than that of *Chiropterotriton.*

The species *Chiropterotriton dimidiata,* associated with *Parvimolge townsendi* by Dunn (1922:5) and later described as new by Taylor (1940:408), is obviously a *Chiropterotriton.* Its myology is less generalized and the origin of the hyoglossus is typically that of *Chiropterotriton.*

The myology of the salamanders in the genera *Magnadigita* and *Bolitoglossa* is, with the exception of *occidentalis, striatula* and *rufescens,* of a generalized nature and I have been unable to discover a single myological character that would serve to separate all of the species of *Magnadigita* from those of *Bolitoglossa.* The presence of the rectus cervicis lateralis in all but two of the species of *Magnadigita* and its absence in all of the *Bolitoglossa* examined, save *mexicana,* is probably the most reliable character. In general the intermandibularis anterior is relatively shorter and less extensive in *Magnadigita* than in the *Bolitoglossa.*

The genera *Magnadigita* and *Bolitoglossa* have in common the following characters: (1) the suprapeduncularis is noticeably wider than long in most species and (2) there is a large mass of pharyngeal fibers between the suprapeduncularis and the deep slip of the rectus cervicis at least in the less specialized forms. The most significant difference between these two genera and the other genera of the family studied is the shape of the proximal end of the ceratohyal. In other Mexican and Central American genera of plethodontids the proximal end of the ceratohyal is noticeably extended anterior to the suprapeduncularis and is either flattened or attenuated, whereas in *Magnadigita* and *Bolitoglossa* the ceratohyals are not extended, or only slightly so, and terminate in a bluntly rounded end only slightly anterior to the suprapeduncularis muscle. This bluntness of the ceratohyals is, as far as I have been able to discover, the most reliable of the throat characters for the separation of these two genera from other Mexican and Central American plethodontids.

The genus *Oedipina* includes a highly specialized series of species not closely related to any of the other genera studied. Although there are variations in nearly all characters examined, the more significant characters are as follows: The quadrato-pectoralis arises from the posterior edge and the ventral surface of the squamosal, and from the lateral edge of the otic capsule deep to the anterodorsal edge of the squamosal. Furthermore, the origin of this muscle is noticeably dorsal to the tip of the quadrate. This condition is unique not only to the Plethodontid salamanders of Mexico and Central America, but also to the remainder of the family Plethodontidae.

A second difference is in the wide and divided origin of the geniohyoideus lateralis. An approach to this condition is found in some *Chiropterotriton* but with this important difference: the fibers arise from the posterior edge of the mandible while in all *Oedipina* the fibers are attached to the ventral surface of the mandible. Furthermore, the medial fibers extend deep to the lateral fibers in *Oedipina* while in *Chiropterotriton* the two parts join and extend caudad as a series of parallel fibers. This I consider a case of homoplassy. The geniohyoideus medialis has an extremely narrow but thicker origin than I have found in other genera. The medialis is always inserted a short distance lateral to the midventral line.

A third difference is found in the division of the rectus cervicis into three nearly equal segments. The posterior segment is approximately equal to the anterior and the middle segment is only slightly shorter than either of the others. This condition is obviously a specialization, since in the generalized genera the posterior segment is as long as the combined lengths of the two other segments.

The genus *Oedipina* is also distinct in having a large suprapeduncularis muscle in which the posterior fibers are as long as or longer than, the anterior or medial fibers. The subarcualis rectus 1 is different from other genera studied in that the muscle has presumably become divided into two heads. A small elongate anterior head and a larger posterior head. The muscle is also noticeably shortened.

The ceratohyals are also distinctive not only in having the proximal end attenuated, but also in lacking the medial lobes which in other genera constrict the posterior portion of the suprapeduncularis.

The species *Lineatriton lineola* is obviously not closely related to the species of the genus *Oedipina*. It does not resemble *Oedipina* in one of the characters listed above and is, as previously stated, myologically more closely related to the genera *Pseudoeurycea* and *Parvimolge* than to any of the other genera studied.

The genus *Thorius* differs noticeably from other Mexican and Central American plethodontids in that all species have lost the intermandibularis anterior and the rectus cervicis lateralis. The subarcualis rectus 1 is shorter than in other Mexican and Central

American genera and the gularis is caudad to the posterior tip of the mandible in all species examined.

The attenuated, rodlike anterior end of the ceratohyal is unique in this genus and although the condition in *Oedipina* approaches that of *Thorius* the shape of the ceratohyals in the two genera is distinctly different and does not serve to relate the two genera.

While there are noticeable myological differences among the various genera of plethodontid salamanders there are also many similarities, particularly in the throat anatomy of the species I consider to be generalized. As previously stated I consider the genus *Pseudoeurycea* to be the most primitive of the Mexican and Central American plethodontids. The generalized conditions of the throat are not only reflected in the myology, but are also evident in the hyobranchial cartilages. A comparison of the throat myology of *Pseudoeurycea bellii* with that found in *Magnadigita robusta* and *Bolitoglossa platydactyla* indicates these species to be very similar, particularly in the following muscles: quadrato-pectoralis, depressor mandibulae, geniohyoideus medialis, geniohyoideus lateralis, interhyoideus, intermandibularis posterior and in the subarcualis rectus 1. Furthermore, the rectus cervicis superficialis reaches the lateral edge of the profundus at the first myocomma anterior to the sternum and the hyoglossus is similar in all three species. Other species in these genera such as *Pseudoeurycea smithi, Magnadigita subpalmata* and *Bolitoglossa flaviventris* are also similar in the general pattern of the throat myology and are only slightly more specialized than the previous species.

Because of these conformities I regard the species *Pseudoeurycea bellii, Magnadigita robusta* and *Bolitoglossa platydactyla* to be representatives of the generalized species in their respective genera.

The establishment of a criterion of generalized species has given a standard for measuring the degree of specialization in other species. One muscle in which specialization is easily followed from the generalized to the specialized species is the quadrato-pectoralis. This muscle arises entirely from the quadrate in *Pseudoeurycea bellii*, and chiefly from the quadrate in *Magnadigita robusta* and *Bolitoglossa platydactyla,* but with a few fibers arising from the squamosal in the last two species. In several species of each genus the quadrato-pectoralis arises almost equally from the quadrate and squamosal. In the specialized species of *Pseudoeurycea cochranae, Magnadigita dunni* and *Bolitoglossa rufescens* the origin of this muscle has shifted dorsally and arises only from the squamosal. In the other genera of Mexican and Central American plethodontids this muscle originates principally or entirely on the squamosal. Thus there appears to be an orthogenetic type of development for the origin of this muscle.

The subarcualis rectus 1 is relatively longest in the primitive species of the Mexican and Central American plethodontids and shortest in the specialized species of *Oedipina* and *Thorius*. In *Hydromantes* this muscle is comparable to that found in the most generalized of the Mexican and Central American species.

The rectus cervicis is similar in the generalized species. In such species the muscle is divided into three unequal segments the posterior of which is as long as the combined lengths of the other two and the superficialis muscle reaches the lateral edge of the profundus at the first myocomma anterior to the sternum. In the more specialized species of *Pseudoeurycea, Magnadigita, Bolitoglossa* and in particular, all species of *Oedipina,* the segments are nearly equal in length and the superficialis does not reach the lateral edge of the profundus.

The median and distal parts of the ceratohyal are very similar throughout all the genera except *Oedipina.* There are variations in the size of the medial lobe and in the angle of the distal hook but otherwise the ceratohyals are essentially the same. The proximal end of the ceratohyal has been variously modified in all genera of Mexican and Central American plethodontids. The primitive condition was presumably spatulate or at least with an enlarged lobe of thin cartilage. I consider the proximal part of the ceratohyals of *Pseudoeurycea, Parvimolge,* and *Lineatrition* to be most similar to the presumed ancestral condition, *Chiropterotriton* is only slightly modified from the ancestral type. The major specializations have taken place in two directions, toward a loss of the proximal lobe in *Magnadigita* and *Bolitoglossa* and toward an attenuation in *Oedipina* and *Thorius.*

I have previously spoken of the broad insertion of the transverse muscles as indicative of primitiveness in *Pseudoeurycea.* In *Magnadigita* and *Bolitoglossa* the insertions of these muscles in the generalized species are also broad, but less so than in *Pseudoeurycea.* There is also a similarity in that the gularis covers the posterior tip of the mandible in the generalized species of all three genera. The intermandibularis anterior has, as in the case of the proximal end of the ceratohyal and in contrast to the quadratopectoralis, become variously modified in the genera of the Mexican and Central American plethodontids. In *Pseudoeurycea* there is an indication that the intermandibularis is being reduced, or even lost in some species, while in others the muscle is large and is becoming much enlarged medially, as in some *Chiropterotriton.* In the species of *Bolitoglossa* and *Magnadigita* I have found the intermandibularis anterior to be a relatively small muscle when compared with *Pseudoeurycea gigantea* and an even smaller muscle when compared with *Pseudoeurycea leprosa* or with any of the species of *Chiropterotriton.* In the species of *Chiropterotriton* the anterior muscle is large, reaching its highest development as a triangular shaped muscle in *terrestris* and *multidentata.* In *Parvimolge* this muscle is well developed, but does not reach the relative size of that in some *Chiropterotriton.* In *Magnadigita* the muscle has become shortened and narrowed. This is also true for *Bolitoglossa flaviventris.* In *Bolitoglossa striatula* and *Bolitoglossa rufescens* the muscle has become much elongated and is narrow medially. The relative size and shape of the intermandibularis anterior was undoubtedly present in the ancestral stock of these salamanders. Two divergent evolutionary trends are obvious, either a reduction in size leading to its final loss or to an enlargement.

In spite of the obvious difference in the ceratohyals of the various genera and in the modification of the intermandibularis anterior, the rectus cervicis lateralis and the suprapeduncularis, the generalized species are very similar myologically and represent the primitive conditions which existed in the primitive stock of the Mexican and Central American Plethodontidae. These data have led me to conclude that these genera arose from similar ancestral stock, whose characteristics were: that the quadrato-pectoralis was originally attached only to the quadrate; that the intermandibularis was present in the ancestral stock; that the subarcualis rectus 1 was greatly elongated and specialized; that the proximal end of the ceratohyal was originally spatulate; that the rectus cervicis was divided into three unequal segments, the posterior of which was approximately as long as the combined lengths of the other segments; and that the rectus cervicis lateralis was well formed.

By utilizing both the differences and conformities that exist or are extant, it is possible to arrange the Mexican and Central American genera into the following series of related groups:

Group I
  *Pseudoeurycea*
  *Chiropterotriton*
  *Parvimolge*
  *Lineatriton*

Group II
  *Magnadigita*
  *Bolitoglossa*

Group III
  *Oedipina*

Group IV
  *Thorius*

The fact that some genera are grouped together does not invalidate their distinctness as genera. The groups are a means of showing what I have concluded to be the lines of descent among the Mexican and Central American salamanders.

## PHYLOGENETIC CONSIDERATIONS

Besides fulfilling the purpose of this investigation, the study has added materially to our understanding of the throat anatomy of the Plethodontidae, and has provided a much broader picture, not only of the Mexican and Central American forms, but also of the entire family.

This study has confirmed many opinions concerning the phylogenetic position of the salamanders of these genera. It has, however, shown that some opinions must be discarded or viewed with considerable doubt. Though there are varying opinions regarding the taxonomy of these salamanders, I am convinced that at least eight, and possibly nine, genera must be recognized. These conform to those listed by Taylor (1944), and are characterized not only by the characters used by Taylor (*op. cit.*) but also by the characteristics of the throat anatomy brought to light by this investigation. It is not impossible that further generic separation will be necessary when the Mexican and Central American Plethodontidae are more completely known.

The Mexican and Central American Plethodontidae here considered are similar in that all have a free tongue, a character I consider to have been established in the ancestral stock before its migration into Mexico. The primitive characteristics of the genus *Gyrinophilus* of eastern United States as indicated by Dunn (1926:27) and Piatt (1935:227) suggest that the ancestral free-tongued species had a very early origin. There is no way of knowing exactly when such a character arose; however, if we accept the Pliocene as stated by Dunn (1926:32) as a possible time of migration, then it is seemingly safe to assume the Miocene as a possible time for its development. The character must have been extant sometime before the invasion of Mexico by the plethodontid salamanders. Furthermore, there is in the free-tongued species a great diversity of other characters in the genera, from the primitive genus *Gyrinophilus*, having many salamandridlike characters, to the highly specialized species of the genera *Oedipina* and *Thorius*. I am convinced that the data thus far gathered by other workers and those resulting from these investigation indicate a very early beginning for the free-tongued condition in the Plethodontidae.

I can find no valid reason for accepting two separate origins for the character of a free tongue in these salamanders. Piatt (1935: 235) has suggested that the genera of his *Gyrinophilus* group had an origin quite apart from the genus *Hydromantes* and likewise from the genera of Mexico and Central America. The idea of a separate origin is based primarily on the presence of the lingual cartilage in the *Gyrinophilus* group, a character thought to be homologous to the "sehnenplatte" of the Salamandridae. Though the lingual cartilage may serve directly to relate the *Gyrinophilus* group to the primitive conditions found in *Salamandra,* it does not suggest (to me at least) an origin for this group separate from that of other free-tongued Plethodontids. The *Gyrinophilus* group and part of the Mexican and Central American genera (*Pseudoeurycea, Parvimolge, Chiropterotriton, Oedipina, Lineatriton,* and *Thorius*) are all characterized by the presence of a sublingual fold. This fold is attached to the floor of the mouth in almost the same position as the tissue used to attach the tongue in such genera as *Plethodon* and may represent a retention of this tissue in the free-tongued forms. In other words, the sublingual fold relates the two major groups which Piatt would derive separately on the basis of a lingual cartilage. Furthermore, *Gyrinophilus* and *Hydromantes,* two quite different genera, are similar, as well as primitive, in that both possess double premaxillae. I am not contending that the two genera listed are closely related, but the character of double premaxillae does indicate that they may have stemmed from a similar ancestry. The hyobranchial apparatus and its musculature are similar and, as suggested by Piatt (1935:234), "give morphological evidence of community of descent at a very early date."

The presence of the lingual cartilage in *Gyrinophilus* definitely indicates a primitive condition referable to a direct descent from the ancestral plethodontid stock. Its absence does not, however, mean that the cartilage could not have been lost in certain groups after the development of the free-tongued condition. Piatt (1935:236), in attempting to relate *Batrachoseps* to *Hydromantes* and *Oedipus,* states, "The os thyreoideum in *Batrachoseps* is much more reduced than in *Gyrinophilus* and could, I think, be explained as a foreshadowing of the conditions in *Hydromantes* and *Oedipus.*" If it be possible to postulate close relationship between genera having a second basibranchial to those without such a bone, then it is just as reasonable to postulate relationships between groups with a lingual cartilage to those without such a cartilage. I am not attempting to suggest a close relationship but rather to emphasize an early relationship among the free-tongued plethodontid salamanders.

The ancestral stock gave rise, then, to two diverging groups of genera. One of these is the *Gyrinophilus* group, including *Gyrinophilus,* the one most nearly approximating the ancestral stock of the line and including *Pseudotriton, Eurycea,* and *Manculus.* The other line includes all other genera of free-tongued salamanders, all of which have arisen from an ancestral stock presumably similar to that of *Gyrinophilus,* but which have, because of migration, isolation, adaptation, and possibly other causes, become highly modified from the ancestral stock. In the second group the os thyreoideum and the omohyoideus have been lost, and the intermandibularis anterior has been retained. The ceratohyals have been modified anteriorly, the first ceratobranchial is smaller than the second, and there has been a noticeable enlargement in the size of the quadrato-pectoralis. A further specialization is apparent in the development of enlarged subdigital pads under the distal phlanges, or in the webbing between the toes, or in both.

The ancestral stock of the Mexican and Central American plethodontids appears to have been divided early into two of the present day lines. The one line is distinct from the other in the retention of a distinct sublingual fold (Taylor 1944:203), a primitive characteristic and one which relates the group more directly to the main line of descent. This branch includes the genera *Pseudoeurycea, Parvimolge, Chiropterotriton, Oedipina, Lineatriton,* and *Thorius.*

The other line includes *Bolitoglossa, Magnadigita,* and possibly *Hydromantes,* although the last genus is primitive and has unquestionably been separated from the other two genera for a greater length of time. These genera are similar in that all have lost the sublingual fold, and the first ceratobranchial is smaller than the second. The myology of *Hydromantes* is more nearly similar to that of some *Magnadigita* or *Bolitoglossa* than to that of other Mexican and Central American species. In *Hydromantes* the omohyoideus and rectus cervicis lateralis are both absent, the suprapeduncularis is similar to that of *Bolitoglossa platydactyla,* and the subarcualis rectus 1 is also very similar in length and origin. The depressor mandibulae is distinctly divided into two muscles and has a similar origin and insertion in all. There are commonly thirteen costal grooves in all three genera.

There are, however, many fundamental differences between *Hydromantes* and the other two genera. In *Hydromantes* there are two premaxillae; the paravomerine teeth are separated from each other by a distinct space; the first basibranchial is flattened medially and proximally and is devoid of cornua; the ceratohyal is attached to the dorsal tip of the quadrate rather than to the squamosal; the quadrato-pectoralis arises entirely from the distal end of the ceratohyal and is closely associated with the interhyoideus; the intermandibularis anterior is absent; the gularis, though distinct and similar in origin and insertion, is noticeably smaller, and the tail is not constricted at its base. This list of characteristics clearly indicates the primitive condition of *Hydromantes,* and although its relationships are with *Magnadigita* and *Bolitoglossa,* there is good reason to believe that the genus *Hydromantes* became isolated from the parental stock of the *Bolitoglossa* line soon after its origin.

As previously indicated, the genera *Magnadigita* and *Bolitoglossa* are closely related. The throat anatomy is generalized and similar, varying so slightly that no single character will serve to separate them. In both genera the ceratohyals are similarly modified, the vertebrae are amphicoelous, and both have prefrontal bones. They are different in that the feet of the *Bolitoglossa* are fully webbed or have at most only the sharp extreme tips of the fingers and toes free. The palms and soles are smooth, and the subdigital pads are lacking under the distal phalanges. In the genus *Magnadigita* the digits of hand and foot are widely spread; the proximal phalanges are included in a heavy webbing; The distal phalanges are free, truncate, and have the subdigital pads well developed. The two middle digits are relatively shortened, giving the appearance of a shorter, more stubby hand or foot than is found in other genera.

The feet of both *Magnadigita* and *Bolitoglossa* are adapted for an arboreal type of life, although there are one or more species in each of the two genera which are presumably terrestrial. The species of the genus *Bolitoglossa* are more specialized in foot type than are the species of *Magnadigita.* In smaller species of *Bolitoglossa,* such as *occidentalis* and *rufescens,* the tail is much shorter than the combined lengths of head and body, the costal grooves are entirely obliterated in most specimens, and the digits are inclosed in a very heavy padlike webbing. The myology of the throat is strikingly different from that of most *Bolitoglossa,* and the first epibranchial is slightly reduced in length. The species *Bolitoglossa* *rufescens* is more closely related to *occidentalis* than to other *Bolitoglossa.* These two species differ chiefly in that the maxilla is toothless in *rufescens* and toothed in *occidentalis* (Taylor 1941: 145): otherwise they are similar. They are certainly the most specialized and divergent species of the genus, and it is questionable whether one should include these species in the genus *Bolitoglossa.*

The other large branch of the Mexican and Central American plethodontids, (*Pseudoeurycea, Parvimolge, Chiropterotriton, Lineatriton, Oedipina,* and *Thorius*) became divided into three divergent evolutionary lines, designated hereafter as the *Thorius* line, *Oedipina* line and the *Pseudoeurycea* line.

The phylogenetic position of the genus *Thorius* is less certain than that of any of the other Mexican and Central American genera, chiefly because it is the most divergent and specialized of the genera. Since its description and its elevation to family rank by Cope (1869), the genus has been subject to more taxonomic changes than any of the genera described for that region. This in itself is indicative of the uncertainty on the part of previous workers of the actual status of the *Thorius* line. Taylor (1944:192-197) has given a rather detailed history of the genus to that date. Since then Smith and Taylor (1948:16) have placed the genus *Thorius* in the subfamily Thoriinae. This later arrangement is based not only on the marked divergences in the external, dental, and skull characters, but also on the opisthocoelous type of vertebral articulation found in the genus. There is, however, no doubt concerning the distinctiveness of the genus from all other free-tongued plethodontids, and I am convinced that the species of this genus are not, as suggested by Dunn (1926:33), closely related to *Parvimolge townsendi* or *Chiropterotriton nasalis.* I have not seen *Chiropterotriton picadoi* and can offer no opinion on its relationship.

The genus *Thorius* differs strikingly from all the plethodontid salamanders of Central America and Mexico. The following characters are unique in this genus: an orbitolabial groove not intercepted by a notch; edentate maxillae in all species; the invariable absence of both the intermandibularis anterior and the rectus cervicis lateralis; a small posterior lobe for the attachment of the quadrato-pectoralis present on the squamosal; the proximal end of the ceratohyal attentuated and rodlike; the dorsum of the skull not ossified; and the vertebrae opisthocoelous rather than amphicoelous. In the light of all these differences, the myological similarities between *Thorius* and such genera as *Pseudoeurycea, Parvimolge* and *Chiropterotriton* seem susceptible to interpretation as a case of convergence, although the myological similarities and the presence of the sublingual fold might, on equally logical grounds, be assumed to reflect genetic homogeny. In spite of all previous studies and new information discovered in the course of my investigation, the phylogenetic position of the genus *Thorius* cannot now be firmly established.

The genus *Manculus* of the Eastern United States has an orbitolabial groove but with this difference: the groove is intercepted by a notch in the lip which extends dorsad near the posterior edge of the eye. In *Thorius* the groove is not intercepted by a notch, but enters the mouth directly. A foreshadowing of the conditions found in *Manculus* is present in *Eurycea,* in which the notch is present but does not completely intercept the groove.

In the genus *Batrachoseps* the median part of the brain case is also membranous, but I do not consider that this character relates the genus *Batrachoseps* to the genus *Thorius.* The two genera are otherwise substantially different, and it appears that the poorly ossified skull is an example of fortuitous convergence. Both genera are terrestrial and subterrestrial in habits and might in this respect have been affected similarly by the environment. In the genus *Batrachoseps* the myology is noticeably different from that of all other genera studied, and I consider its association with *Hydromantes* and the Mexican and Central American plethodontids as suggested by Piatt (1935:232) to be entirely unwarranted. The genus *Batrachoseps* is itself a highly specialized tongue-tied group of salamanders. Its relationships are presumably with the genus *Plethodon* rather than with any of the free-tongued groups.

The relationships of the genus *Oedipina* are seemingly also with those of the Mexican and Central American genera having a sublingual fold. Most of the throat muscles of this genus are more specialized than those of *Thorius,* and moreover *Oedipina* appears to be equally specialized regarding the hyobranchial apparatus. The two genera have undergone specialization in different ways and are widely separated, even though there may be a few rather noticeable similarities in the throat myology of the two genera.

Hilton (1947:38) described the genus *Oedopinola* and designated the Panamanian species *Oedipina complex* (Dunn) as the type species and also included *Oedipina parvipes* (Peters) in the genus. The generic characters presented by Hilton (1946:38) are as follows: "Short snout. Hands and feet without free toes. Single premaxillary with a single long cylindrical shaft before forking caudally. Slight fontanelle. Vertebrae not long, no alar folds. Nineteen vertebrae before the sacral. Carpus and tarsus with a few larger cartilages but mostly smaller." I have dissected both Panamanian species and have found them to be very similar to *Oedipina uniformis* Keferstein in their throat anatomy (Tanner 1950:37). Unfortunately Hilton's comparisons appear to have been made with the species *Lineatriton lineola* and not with any of the species in the genus *Oedipina.* This fact obviously accounts for the many differences observed by Hilton. It is therefore necessary to retain the species *complex* and *parvipes* in the genus *Oedipina* and to place the genus *Oedopinola* Hilton as a synonym under the genus *Oedipina* Keferstein.

The genus *Pseudoeurycea* is the most primitive of the Mexican and Central American plethodontids and as such forms the main stem for the remainder of the genera. The primitive characteristics are reflected not only in the hyobranchial apparatus and its musculature, but also in the entirely free digits of the hands and feet. In the species *P. cephalica* there is a partial webbing of the proximal digits, a condition not found, so far as I am aware, in other species of the genus. Despite the fact that the foot is slightly webbed, the hyobranchial apparatus and the myology of *cephalica*, together with other significant characteristics, are very similar to other *Pseudoeurycea*, and point to no close relationship with other genera.

The genus *Chiropterotriton* appears to have been derived from the genus *Pseudoeurycea.* The origin of the genus has not been recent, however, inasmuch as the genus *Chiropterotriton* has undergone adaptive radiation and its species are specialized. The genus is most similar to the species of group III of *Pseudoeurycea,* and I suspect its origin to be with this group. The two genera differ as follows: the proximal ends of the ceratohyals have been modified; the hyoglossus has become attached to the ventral surface of the basibranchial; the subarcualis rectus 1 has become relatively shorter; and the intermandibularis anterior is present and relatively larger than in most *Pseudoeurycea.* The digits are widely spread, and the proximal phalanges of the hands and feet are enclosed in a webbing.

The throat myology and the hyobranchial apparatus of the genus *Parvimolge* relates it to the *Pseudoeurycea* line. The muscle patterns are more in accordance with those of *Pseudoeurycea* than they are with *Chiropterotriton.* The ceratohyals and the relatively elongate epibranchials are very similar to *Pseudoeurycea.*

However, in the genus *Parvimolge* the fingers and toes are more completely webbed than are those of *Chiropterotriton* and lie close together rather than widely spread as in the latter genus. The middle finger and the middle toe are noticeably longer and are pointed rather than rounded. The foot type is more nearly like that of *Lineatriton* than any other type seen in the Mexican and Central American species.

Dunn (1926) suggested that the species *Parvimolge townsendi* is an annectant form relating *Thorius pennatulus* to the species now considered as belonging to the genus *Chiropterotriton.* I have been unable to find any characters in the throat anatomy that would relate *Parvimolge* directly to either of the above genera or to any other genus of free-tongued Mexican or Central American plethodontids.

The species *Lineatriton lineola* is so similar in its throat anatomy to the genera *Pseudoeurycea, Chiropterotriton* and *Parvimolge* and so different from the genus *Oedipina* that I have found it advisable to associate the genus *Lineatriton* with the *Pseudoeurycea* evolutionary line. A careful comparison of the figures of *L. lineola* (pl. LXIX, fig. E; pl. LXXII, fig. B) with the figures of *O. uniformis* (pl. LXX, fig. D; pl. LXXII, fig. D) will indicate the distinct differences between these two genera. If the figures of *L. lineola* are now compared to the figures of *Pseudoeurycea,* the similarity of *L. lineola* to the species of the genus *Pseudoeurycea* is as obvious as are its differences from *O. uniformis.* Furthermore, the feet of *L. lineola* are not typical of the genus *Oedipina,* but are less webbed and may be compared more favorably with those found in the genus *Parvimolge.*

In view of the differences between the species *L. lineola* and the species of *Oedipina* as regards the throat myology, the hyobranchial apparatus, the hands and feet, the vertebrae, and other significant characters, and the obvious similarities of *L. lineola* to the species of *Pseudoeurycea* line, I cannot regard this species as a member of the genus *Oedipina.* Further anatomical study (Tanner 1950) has pointed to the necessity of describing the new genus *Lineatriton* to receive this species.

The following diagram (Fig. 5) illustrates the opinion herein expressed concerning the phylogeny of the free-tongued Plethodontidae. Although the diagram is based primarily on the throat anatomy, other characters have also been used in arriving at the relationships.

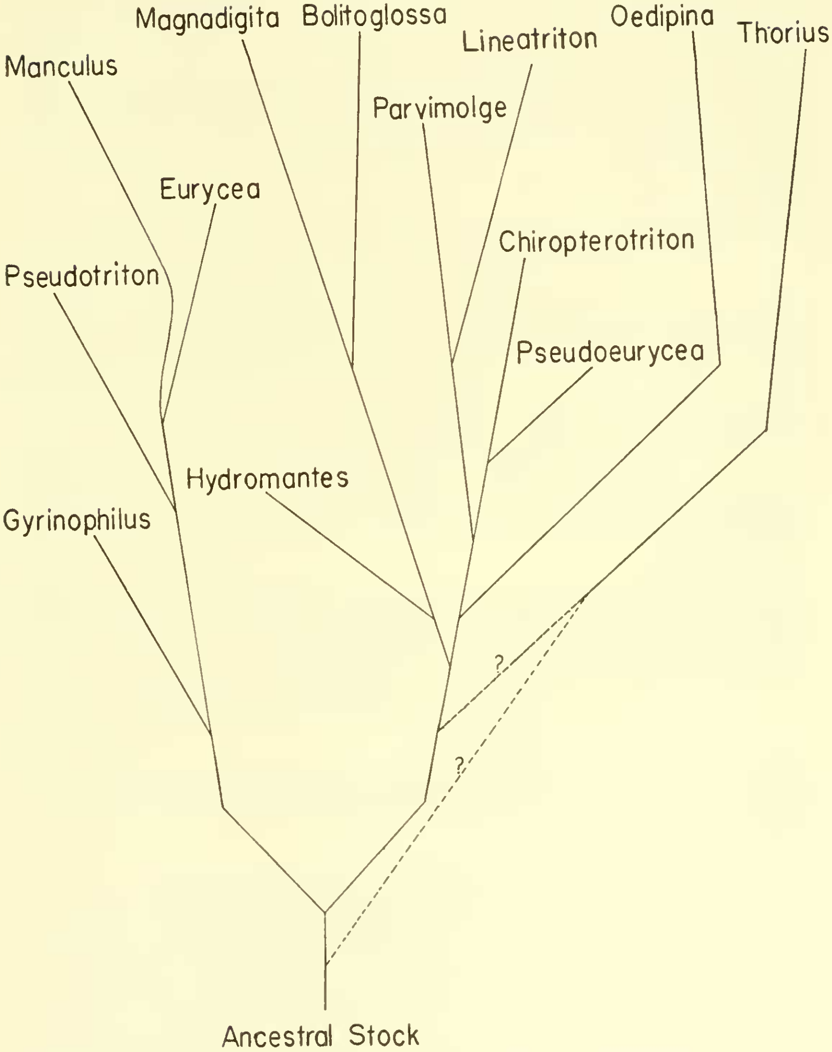

FIG. 5. Phylogeny of the free-tongued Plethodontidae.

## SUMMARY AND CONCLUSIONS

1. The intermandibularis anterior is present in most species and in all genera of Mexican and Central American plethodontids, except *Thorius*.

2. The origin of the quadrato-pectoralis is variable among the species and among the genera. In those species here considered

as generalized, the origin is on the quadrate, whereas in specialized species the muscle arises from the squamosal.

3. The gularis has an extensive origin and an extensive insertion in the generalized species. In specialized species the anterior edge of the muscle is posterior to the caudal tip of the mandible, and the number of fibers inserted in the ventral aponeurosis is greatly reduced.

4. The interhyoideus is rotated at 180 degrees from the origin to the insertion and is distinct from the quadrato-pectoralis in all genera of Mexican and Central American Plethodontidae.

5. The depressor mandibulae is divided into two separate muscles in all genera of Mexican and Central American Plethodontidae and is herein considered as the depressor mandibulae anterior and the depressor mandibulae posterior.

6. The origin of the geniohyoideus lateralis is more variable than that of the geniohyoideus medialis. It is particularly variable in the arboreal species of the genus *Chiropterotriton* and in the genus *Oedipina.*

7. The rectus cervicis is divisible into three unequal segments. In the generalized species the posterior segment is as long as the combined length of the two anterior segments.

8. There is a small medial slip extending deep from the anterior myocomma of the rectus cervicis, which I have designated as the deep slip of the rectus cervicis.

9. A small, narrow muscle, presumably derived from the lateral edge of the rectus cervicis, is described as new and designated the rectus vervicis lateralis.

10. The omohyoideus muscle is not present in the Mexican and Central American genera of free-tongued Plethodontidae.

11. The subarcualis rectus I is highly specialized in all genera studied, but is proportionally longer in the generalized species. In *Oedipina* this muscle has been divided into two heads.

12. The suprapeduncularis is distinctly separated from all pharyngeal fibers and from the deep slip of the rectus cervicis. It is characterized by having the anterior margin indented, giving the appearance of a broad U.

13. In all *Chiropterotriton* the hyoglossus originates on the ventral surface of the anterior tip of the basibranchial. This is considered to be a unique specialization.

14. The second basibranchial (os thyreoideum) is absent in all genera of Mexican and Central American plethodontids. In its place is a connective tissue vestige known as the inscriptio tendinis.

15. The proximal end of the ceratohyal is sufficiently modified in the Mexican and Central American plethodontids to be used as a character in the separation of the genera.

16. There is sufficient evidence in the throat anatomy of the Mexican and Central American genera of plethodontid salamanders to provide a basis for separating them into at least eight genera.

17. It is postulated that the free-tongued condition is homologous among plethodontid salamanders, and that the ancestors of the Mexican and Central American genera were free-tongued before migration to Mexico.

18. On the basis of the throat anatomy the genus *Pseudoeurycea* is the most primitive, whereas the genera *Oedipina* and *Thorius* are the most specialized of all the genera.

19. The species *Lineatriton lineola* has been associated with the generalized genera *Pseudoeurycea* and *Parvimolge.*

20. The species *Chiropterotriton abscondens* and *Bolitiglossa rufescens* are atypical, and represent the extremes of variation within these genera.

21. On the basis of the throat anatomy and other concomitant data, the genera of Mexican and Central American Plethodontidae here recognized are believed to have arisen from similar primitive stock through four separate lines of descent.

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## Key to Abbreviations Used on Plates

### SKELETON

Bb1, first basibranchial.
Cb1, first ceratobranchial.
Cb2, second ceratobranchial.
Ch, ceratohyal.
Cor, cornu.
Eb1, first epibranchial.
Md, mandible.
Sc, sternum.

### MUSCLES

Ah, abdominohyoideus.
Chi, subarcualis rectus 1.
Drc, deep slip of rectus cervicis.
Ghl, geniohyoideus lateralis.
Ghm, geniohyoideus medialis.
Hg, hyoglossus.
Ih, (fig. B) interhyoideus.
Ih, (fig. D) quadrato-pectoralis.
Ina, intermandibularis anterior.
Inpa, intermandibularis posterior anterior slip.
Inp, intermandibularis posterior.
Qp, (fig. D) interhyoideus.
Ra, rectus abdominis.
Rc, rectus cervicis profundus.
Rcs, rectus cervicis superficialis.
Sp, suprapeduncularis.

## PLATE LXVIII

Fig. A. *Chiropterotriton arborea* (Taylor). Transverse and longitudinal ventral throat muscles. E. H. T. No. 16748. × 5.

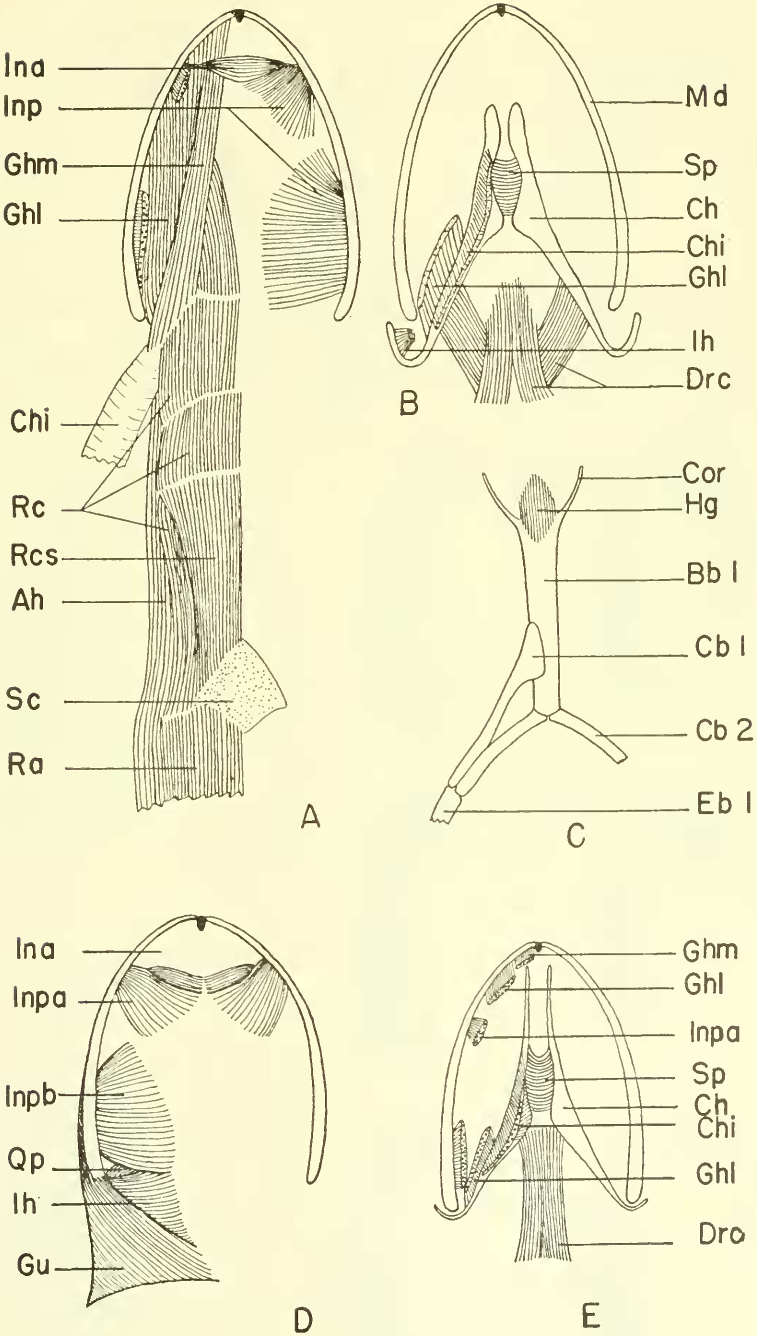
Fig. B. *Chiropterotriton arborea* (Taylor). The deep throat muscles and the ceratohyals. E. H. T. No. 16748. × 5.

Fig. C. *Chiropterotriton multidentata* (Taylor). The branchial cartilages and the M. hyoglossus. E. H. T. No. 25481. × 6.

Fig. D. *Pseudoeurycea rex* (Dunn). Transverse ventral throat muscles. E. H. T. No. 27281. × 5.

Fig. E. *Thorius pennatulus* (Cope). The deep throat muscles and the ceratohyals. E. H. T. No. 25227. × 10.

## PLATE LXVIII



## PLATE LXIX

FIG. A. *Chiropterotriton multidentata* (Taylor). Transverse ventral throat muscles. E. H. T. No. 25481. × 6.

FIG. B. *Pseudoeurycea gigantea* (Taylor). Transverse ventral throat muscles. E. H. T. No. 28910. × 2½.

FIG. C. *Pseudoeurycea goebeli* (Schmidt). Transverse ventral throat muscles. E. H. T. No. 20301. × 4.

FIG. D. *Chiropterotriton terrestris* (Taylor). Transverse ventral throat muscles. E. H. T. No. 23309. × 10.

FIG. E. *Lineatriton lineola* (Cope). Transverse ventral throat muscles. E. H. T. No. 26583. × 7½.

FIG. F. *Parvimolge townsendi* (Dunn). Transverse ventral throat muscles. E. H. T. No. 31572. × 10.

FIG. G. *Chiropterotriton chondrostega* (Taylor). Transverse ventral throat muscles. E. H. T. No. 17297. × 7½.

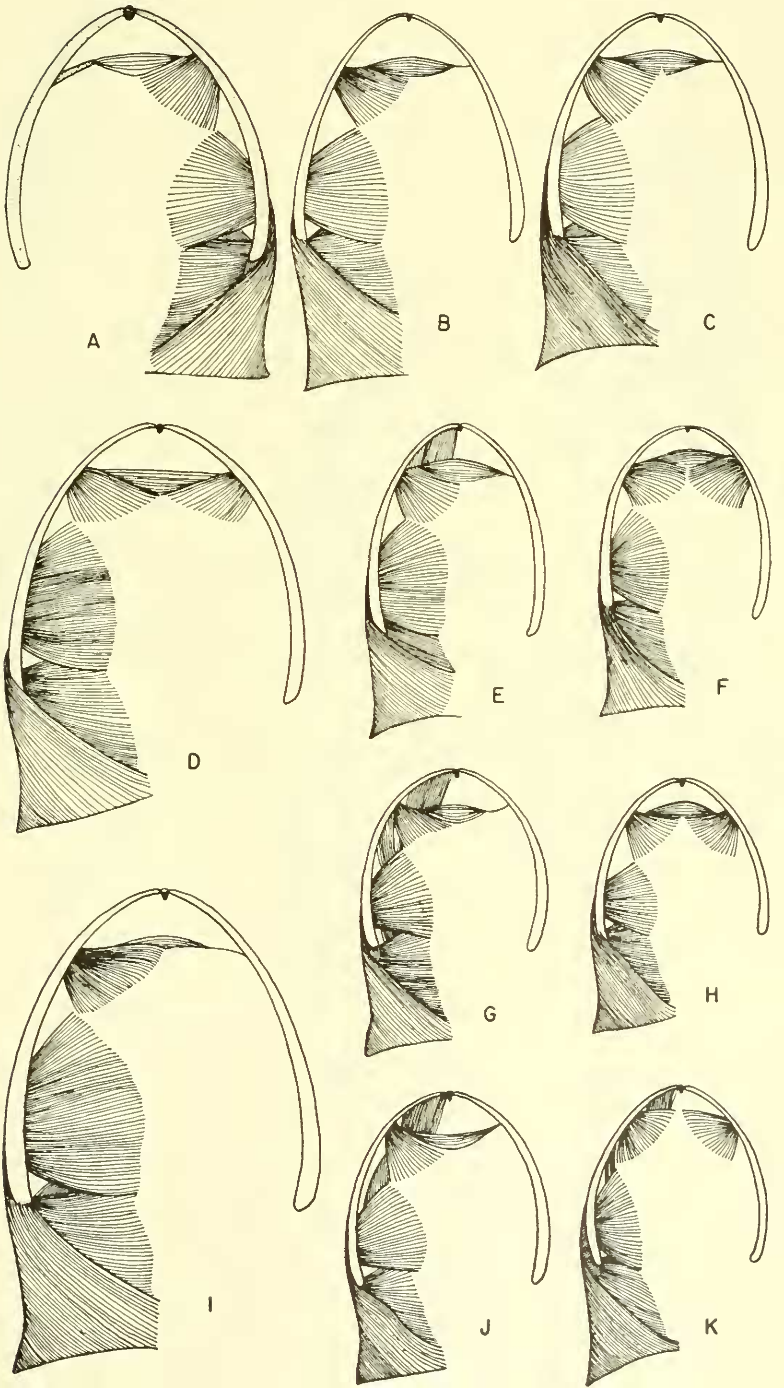
FIG. H. *Chiropterotriton chiroptera* (Cope). Transverse ventral throat muscles. E. H. T. No. 29315. × 5.

FIG. I. *Pseudoeurycea nigromaculata* (Taylor). Transverse ventral throat muscles. E. H. T. No. 24603. × 5.

FIG. J. *Chiropterotriton xolocalcae* (Taylor). Transverse ventral throat muscles. E. H. T. No. 25313. × 5.

FIG. K. *Chiropterotriton abscondens* Taylor. Transverse ventral throat muscles. E. H. T. No. 1410. × 7½.

PLATE LXIX



## PLATE LXX

FIG. A. *Batrachoseps a. attenuatus* (Eschscholtz). Transverse ventral throat muscles. Univ. of Kans. Mus. Nat. Hist. No. 5098. × 7½.

FIG. B. *Magnadigita robusta* (Cope). Transverse ventral throat muscles. E. H. T. No. 25074. × 3.

FIG. C. *Magnadigita nigroflavescens* (Taylor). Transverse ventral throat muscles. E. H. T. No. 26784. × 5.

FIG. D. *Oedipina uniformis* Keferstein. Transverse ventral throat muscles. E. H. T. No. 1021. × 5.

FIG. E. *Parvimolge townsendi* (Dunn). The deep throat muscles and the ceratohyals. E. H. T. No. 31572. × 7½.

FIG. F. *Thorius narisovalis* Taylor. Transverse ventral throat muscles. E. H. T. No. 25041. × 10.

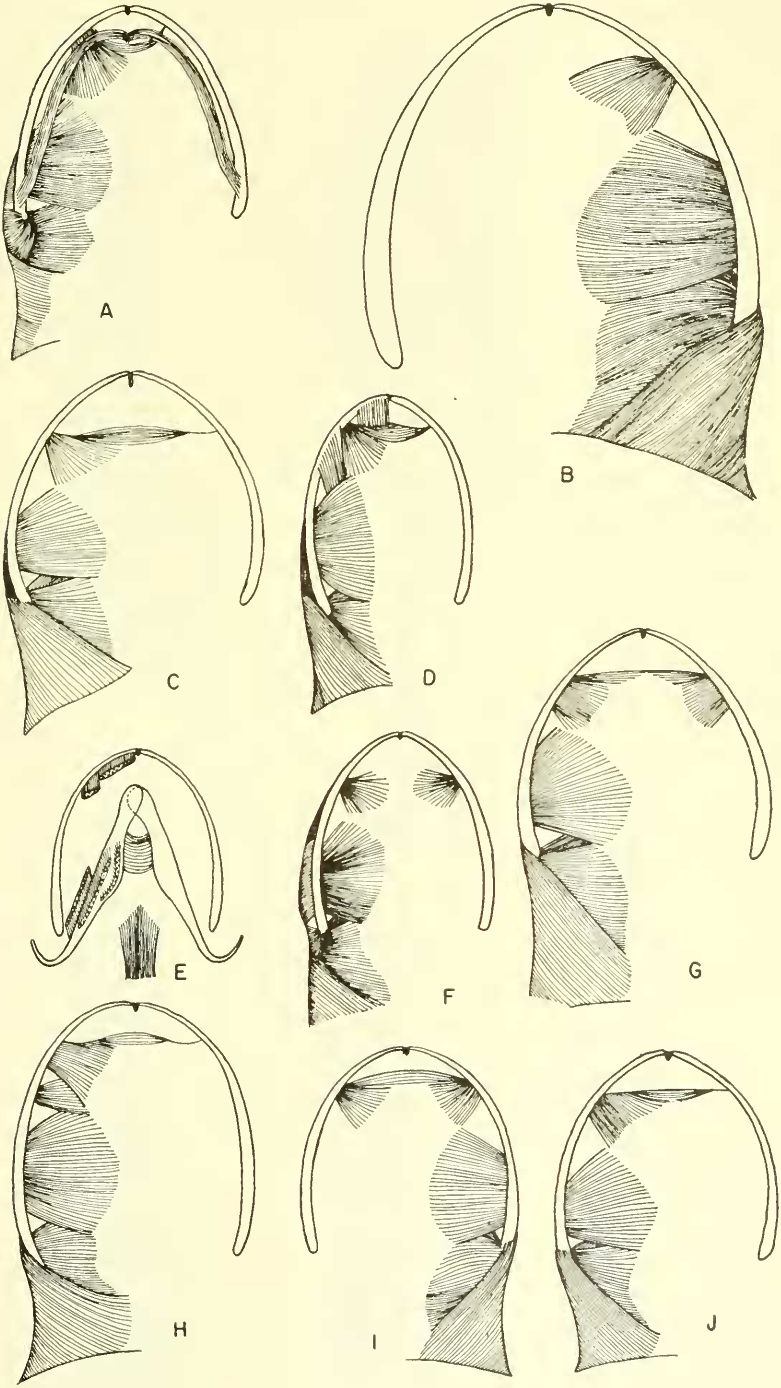
FIG. G. *Bolitoglossa rufescens* (Cope). Transverse ventral throat muscles. E. H. T. No. 18863. × 7½.

FIG. H. *Bolitoglossa flaviventris* (Schmidt). Transverse ventral throat muscles. E. H. T. No. S17076. × 3.

FIG. I. *Bolitoglossa striatula* (Noble). Transverse ventral throat muscles. E. H. T. No. 402. × 4.

FIG. J. *Bolitoglossa occidentalis* Taylor. Transverse ventral throat muscles. E. H. T. No. 28121. × 5.

## PLATE LXX



## PLATE LXXI

FIG. A. *Pseudoeurycea nigromaculata* (Taylor). Longitudinal throat muscles. E. H. T. No. 24603. × 5.

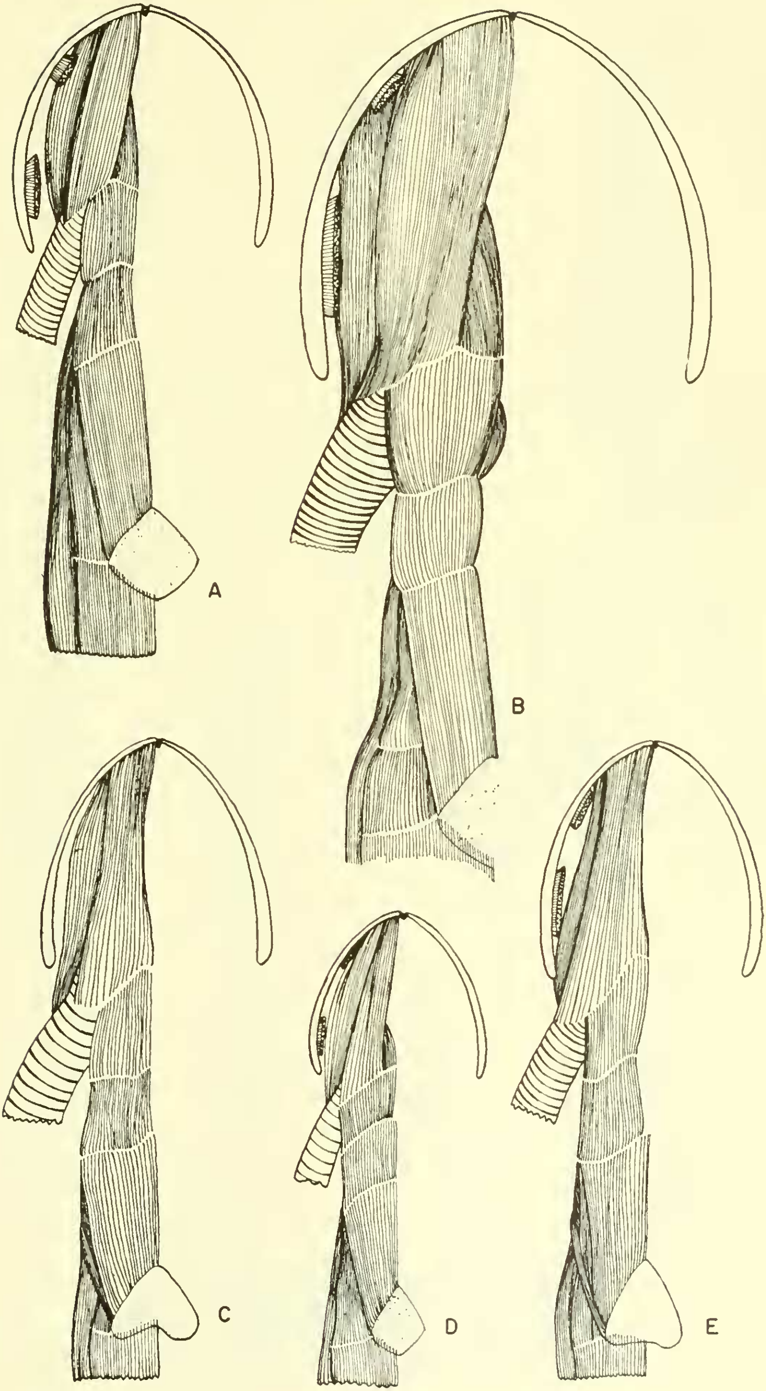
FIG. B. *Bolitoglossa platydactyla* (Cuvier). Longitudinal throat muscles. E. H. T. No. 16321. × 5.

FIG. C. *Pseudoeurycea gigantea* (Taylor). Longitudinal throat muscles. E. H. T. No. 28910. × 2½.

FIG. D. *Chiropterotriton chiroptera* (Cope). Longitudinal throat muscles. E. H. T. No. 29315. × 5.

FIG. E. *Pseudoeurycea goebeli* (Schmidt). Longitudinal throat muscles. E. H. T. No. 20301. × 4.

PLATE LXXI



## PLATE LXXII

FIG. A. *Bolitoglossa striatula* (Noble). Longitudinal throat muscles. E. H. T. No. 402. × 4.

FIG. B. *Lineatriton lineola* (Cope). Longitudinal throat muscles. E. H. T. No. 26583. × 7½.

FIG. C. *Thorius narisovalis* Taylor. Longitudinal throat muscles. E. H. T. No. 25041. × 10.

FIG. D. *Oedipina uniformis* Keferstein. Longitudinal throat muscles. E. H. T. No. 1021. × 5.

FIG. E. *Parvimolge townsendi* (Dunn). Longitudinal throat muscles. E. H. T. No. 31572. × 10.

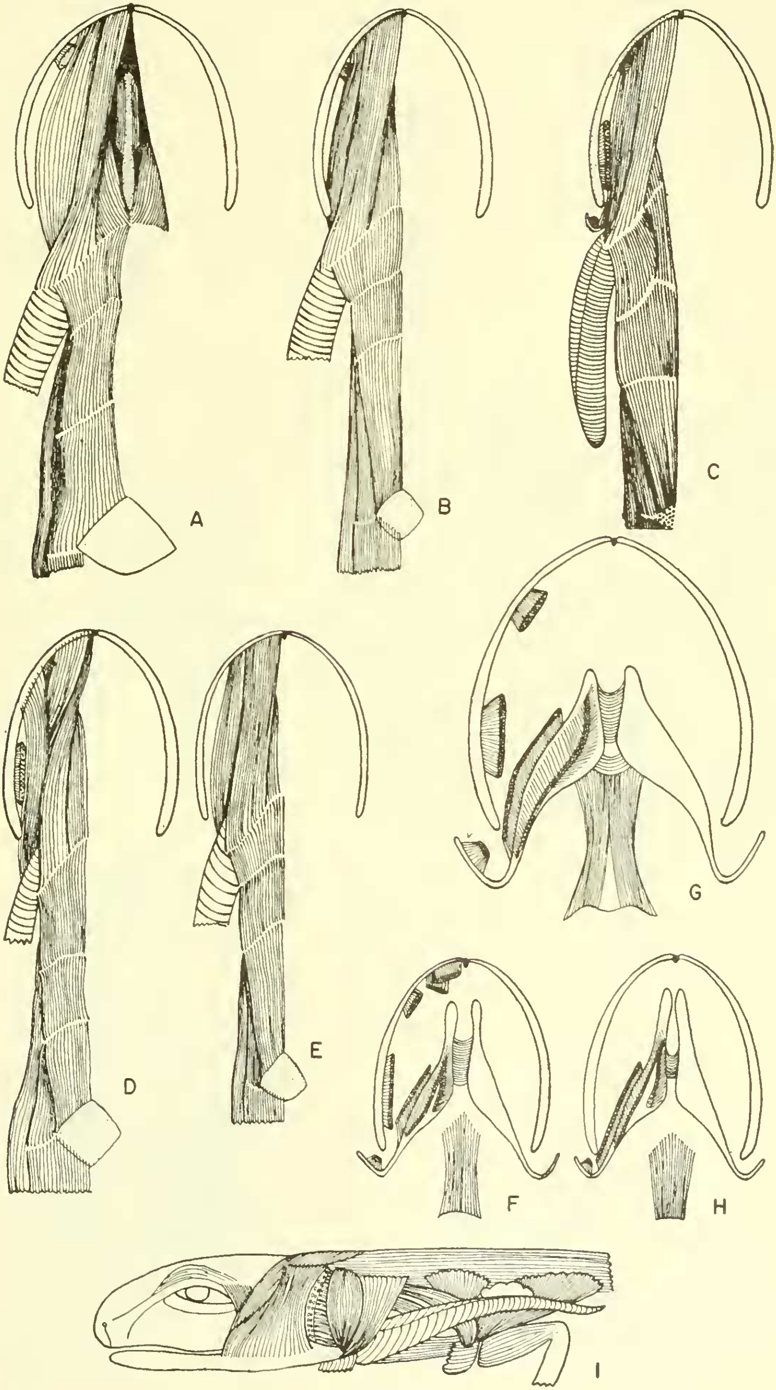
FIG. F. *Pseudoeurycea rex* (Dunn). The deep throat muscles and the ceratohyals. E. H. T. No. 27281. × 5.

FIG. G. *Magnadigita macrinii* (Lafrentz). The deep throat muscles and the ceratohyals. Amer. Mus. Nat. Hist. No. A51823. × 4.

FIG. H. *Lineatriton lineola* (Cope). The deep throat muscles and the ceratohyals. E. H. T. No. 26583. × 7½.

FIG. I. *Bolitoglossa platydactyla* (Cuvier). Lateral view of head and throat muscles. E. H. T. No. 16321. × 2½.

PLATE LXXII



## PLATE LXXIII

FIG. A. *Bolitoglossa rufescens* (Cope). The deep throat muscles and the ceratohyals. E. H. T. No. 18863. × 7½.

FIG. B. *Pseudoeurycea goebeli* (Schmidt). The deep throat muscles and the ceratohyals. E. H. T. No. 20301. × 4.

FIG. C. *Chiropterotriton abscondens* Taylor. The deep throat muscles and the ceratohyals. E. H. T. No. 1410. × 7½.

FIG. D. *Magandigita robusta* (Cope). The deep throat muscles and the ceratohyals. E. H. T. No. 25074. × 7½.

FIG. E. *Pseudoeurycea nigromaculata* (Taylor). The deep throat muscles and the ceratohyals. E. H. T. No. 24603. × 5.

FIG. F. *Bolitoglossa striatula* (Noble). The deep throat muscles and the ceratohyals. E. H. T. No. 402. × 4.

FIG. G. *Bolitoglossa platydactyla* (Cuvier). The deep throat muscles and the tongue. E. H. T. No. 16321. × 5.

FIG. H. *Pseudoeurycea cochranae* (Taylor). The deep throat muscles and the ceratohyals. E. H. T. No. 17727. × 5.

# PLATE LXXIII